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Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species

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Abstract

The presence of an adhesive abdominal sucker (gastromyzophory) allows tadpoles of certain species of anurans to live in fast-flowing streams. Gastromyzophorous tadpoles are rare among anurans, known only in certain American bufonids and Asian ranids. To date, *Huia sumatrana*, which inhabits cascading streams, has been the only Sumatran ranid known to possess gastromyzophorous tadpoles. In the absence of thorough sampling and molecular barcoding of adults and larvae, it has remained to be confirmed whether other Sumatran ranid species living in similar habitats, i.e., *Chalcorana crassiovis*, possesses this larval type. Moreover, the taxonomic status of this species has long been uncertain and its taxonomic position within the Ranidae, previously based exclusively on morphological characters, has remained unresolved. To study the diversity and relationships of these frogs and to establish the identity of newly collected gastromyzophorous tadpoles from Sumatra, we compared genetic sequences of *C. crassiovis*-like taxa from a wide range of sites on Sumatra. We conducted bayesian and maximum likelihood phylogenetic analyses on a concatenated dataset of mitochondrial (12S rRNA, 16S rRNA, and $tRNA^{val}$) and nuclear (RAG1 and TYR) gene fragments. Our analyses recovered *C. crassiovis* to be related to *Clinotarsus*, *Huia*, and *Meristogenys*. The DNA barcodes of the gastromyzophorous tadpoles matched adults from the same sites. Herein, we provide a re-description of adult *C. crassiovis* and propose "*C. kampeni*" as a synonym of this species. The molecular evidence, morphological features, and distribution suggest the presence of two related new species. The two new species and *C. crassiovis* together represent a distinct phylogenetic clade possessing unique molecular and morphological synapomorphies, thus warranting a new genus.

Abstrak

Pada beberapa jenis katak tertentu yang hidup di sungai berarus deras, di bagian abdomen berudunya terdapat semacam alat perekat sebagai mekanisme adaptasi pada kondisi habitat tempat tinggalnya. Tipe berudu seperti ini dikenal dengan nama *gastromyzophorous* dan sangat jarang ditemukan, hanya diketahui pada beberapa jenis bufonid di Amerika dan katak ranid di Asia. Hingga saat ini, hanya *Huia sumatrana*, dengan habitat sungai berarus deras, yang diketahui memiliki tipe berudu seperti ini di Sumatra. Tanpa survey menyeluruh dan tanpa *DNA barcoding* untuk katak dewasa dan kecebong, dugaan men-

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genai keberadaan katak jenis lain dengan tipe berudu serupa di pulau ini, misalnya *Chalcorana crassiovis*, masih harus dibuktikan. Di sisi lain, status taksonomi jenis ini hingga kini masih belum dapat dipastikan, dan posisi taksonominya dalam famili Ranidae hanya berdasarkan karakter morfologi saja. Oleh karena itu, untuk mengetahui keanekaragaman dan hubungan kekerabatan dari katak-katak jenis tersebut, serta untuk memastikan identitas koleksi berudu *gastromyzophorous* dari Sumatra, kami membandingkan data genetik dari semua taxa yang mirip dengan *C. crassiovis* dari berbagai lokasi di Sumatra. Kami merekonstruksi pohon filogeni dengan menganalisis sekuens DNA dari gabungan fragmen gen mitokondria (12S rRNA, 16S rRNA, dan $tRNA^{val}$) dan gen inti (RAG1 dan TYR) menggunakan metode Bayesian dan Maximum Likelihood. Hasil penelitian kami membuktikan bahwa *C. crassiovis* berkerabat dekat dengan *Clinotarsus, Huia*, dan *Meristogenys*. Sekuens DNA dari berudu gastromyzophorous memiliki kecocokan dengan sekuens DNA katak dewasa dari lokasi yang sama. Dalam paper ini, kami menyajikan deskripsi ulang untuk *C. crassiovis* dan menyarankan agar "*C. kampeni*" menjadi junior synonym dari *C. crassiovis*. Bukti molekuler, karakter morfologi, dan kisaran distribusi menunjukkan bahwa terdapat dua jenis baru yang berkerabat dengan *C. crassiovis*. Ketiganya menunjukkan perbedaan filogenetik yang signifikan, yang dibuktikan dengan adanya synapomorphy pada karakter molekuler dan morfologi yang unik. Oleh sebab itu dibentuk genus baru untuk ketiga jenis ini.

Introduction

A fascinating aspect of Southeast Asian ranid frogs is that some of them possess tadpoles with large abdominal suckers. The presence of this adhesive structure has been referred to as gastromyzophory (Inger 1966). Altig and Johnston (1989) described gastromyzophorous tadpoles as an ecomorphological guild. These tadpoles are adapted to live in fast-flowing streams (McDiarmid and Altig 1999, Altig 2006). Their body profile is streamlined with an extended sloping snout. Their adhesive abdominal sucker allows them to cling to rocks even in the fast-flowing, turbulent water of cascades (Nodzenski and Inger 1990, Gan et al. 2015). The abdominal sucker occupies almost the entire ventral surface of the body immediately posterior to the oral disk; both act together to press the body to the substrate through suction. The sucker has raised thickened lateral and posterior rims that seal against the substrate; the oral disk itself is broadly expanded to almost full body width. On the ventral surface of this sucker, there are spots or bands of brown skin, i.e., keratinized epithelium, probably enhancing friction when the sucker engages with the rock surface (Inger 1985, Gan et al. 2015). The tadpoles are able to loosen the suction momentarily to drag themselves forward by action of their strongly developed jaws; algae and other organic rock overgrowth is scraped off by the jaws and keratodont rows of the oral disk while wandering over the rock surface (Inger 1966, AH pers. observ.). According to our field observations on Bornean *Meristogenys* tadpoles (AH unpubl.), this feeding mode restricts taxa with gastromyzophorous tadpoles to certain habitats and microhabitats: clear rocky streams with considerable water velocity and enough light reaching those rocks to form organic overgrowth for the tadpoles to graze on.

Members of the gastromyzophorous tadpole guild are relatively rare among anurans. They are known only in certain bufonids (e.g., Rao and Yang 1994, Boistel et al. 2005, Matsui et al. 2007, Aguayo et al. 2009, Rueda-Solano et al. 2015) and some Asian ranids: species of *Amolops* Cope, 1865, *Huia* Yang, 1991, *Meristogenys* Yang, 1991, and *Rana sauteri* Boulenger, 1909 (Kuramoto et al. 1984, Yang 1991, Malkmus et al. 2002, Matsui et al. 2006, Ngo et al. 2006, Shimada et al. 2007, Stuart 2008, Gan et al. 2015).

In Asia, *Amolops*, *Huia*, and *Meristogenys* are all genera for which the tadpoles are known to have the gastromyzophorous type (Inger 1966, Yang 1991, Shimada et al. 2015): a total of 69 species are currently listed for these genera (Frost 2017). All adult frogs of this group were mainly recorded along swift rocky hill or mountain streams in forested areas. These frogs usually like to perch themselves on rocks or vegetation in the vicinity of streams. In case of *Meristogenys*, it has been reported that eggs are glued to rock surfaces to keep them from being washed away (Malkmus et al. 2002). In Sumatra, this aforementioned habitat for ranid species with gastromyzophorous tadpoles is very abundant due to the mountainous tolopogy, which stretches longitudinally along the island. To date, *Huia sumatrana* Yang, 1991 has been the only Sumatran ranid positively known to possess gastromyzophorous tadpoles (Yang 1991, Manthey and Denzer 2014). The tadpoles of *H. modigliani* (Doria, Salvidio & Tavano, 1999), a species also recorded from Sumatra, remain unkown. In an extensive field effort, we focused on sampling riverine ranids from fast-flowing or torrential streams. We suspected that there might be species, other than *H. sumatrana*, that inhabit torrential stream habitats in Sumatra and also possess gastromyzophrous larvae. In fact, one of us had found unidentified gastromyzophorous tadpoles in Su-

matra in previous fieldwork (DI unpubl.). It has been known that particularly *Odorrana hosii* (Boulenger, 1891), *Chalcorana crassiovis* (Boulenger, 1920), and/or *C. kampeni* (Boulenger, 1920), are Sumatran ranid species that occur in rocky, fast flowing streams, along with *H. sumatrana*. Potentially, as inferred from the preferred habitat of adults, these taxa could all be candidates for possessing gastromyzophorous tadpoles. The tadpoles of *O. hosii*, however, show that such habitats offer various microhabitats options. The tadpole of *O. hosii* have no abdominal sucker and live in relatively quiet, leaf litter filled side-pools (Inger 1966, Grossmann and Manthey 1997, AH pers. observ.). In case of *C. crassiovis* and/or *C. kampeni,* no information regarding tadpoles is hitherto available and the possibility of a gastromyzophorous tadpoles has remained unverified until now.

Chalcorana crassiovis (Boulenger, 1920) was originally described as *Rana crassiovis* Boulenger, 1920 based on two specimens (BMNH 1947.2.3.99 and BMNH 1947.2.4.1) collected from Kerinci, Sumatra, Indonesia at ~1219 m (4,000 ft.) a.s.l.. In the same publication describing *C. crassiovis*, Boulenger (1920) also re-described *Rana pantherina* van Kampen, 1910 as *R. kampeni*. The short original description of *R. pantherina* by van Kampen (1910) included a figure of one specimen. Boulenger (1920) based his description of *C. kampeni* on a specimen (ZMA unregistered number) collected at Bandar Baru, Batak Mts., Kabupaten (=Regency) Dili Serdang, Provinsi (=Province) Sumatera Utara at ± 900 m a.s.l.. Van Kampen (1923) later recorded another population of *C. kampeni* from Serepai and Sungai Kring in Kerinci. Van Tujil (1995) declared the holotype of *C. kampeni* as lost.

Inger and Iskandar (2005) were the first to report on a large series of *Chalcorana crassiovis* from along the banks of Batang Tarusan, Provinsi Sumatera Barat and provide a re-description of *C. crassiovis* on the basis of these samples. The original description of *C. kampeni* was very similar to that of *C. crassovis* leading Inger and Iskandar (2005) to doubt the validity of *C. kampeni* and to conclude that it may be conspecific with *C. crassiovis*. Inger and Iskandar (2005) considered the larger tympanum of *C. kampeni* only a sexual dimorphism within *C. crassiovis*; judging by its small reported size (36.5 mm, van Kampen 1910), the *C. kampeni* type specimen was probably a male. Despite the conclusion of Inger and Iskandar (2005), the two taxa have not been synonymized and some authors have maintained the name *C. kampeni* and applied it to all known populations previously referred to as *Rana kampeni* (e.g., Frost et al. 2006, Che et al. 2007, Oliver et al. 2015).

To date, no studies have included *Chalcorana crassiovis* (or *C. kampeni*) in a molecular phylogenetic context, and few have included Sumatran congeners (Inger et al. 2009, Pyron and Wiens 2011, Oliver et al. 2015, Chan and Brown 2017). Sound phylogenetic hypotheses based on robust sampling of the *Chalcorana* group remain to be proposed. This is significant given the ensuing debates over the relationships among the Asian Ranidae in recent decades. After its original description by Boulenger (1920) as *Rana crassiovis*, this species has been placed in various genera (i.e., *Hydrophylax* (Frost et al. 2006), *Hylarana* (Che et al. 2007), and *Chalcorana* (Oliver et al. 2015)) on the basis of secondary taxonomic implications from analyses of other, putatively related taxa (Frost 2017). This past history of various placements clearly shows that *C. crassovis* needs to be analyzed in a larger phylogentic context amongst ranids. Phylogenetic analyses of new data have the potential to significantly contribute to the ongoing discussion and ultimately lead to more stable taxonomic amendments.

Considering the confusing and unstable taxonomic history of *Chalcorana crassiovis* and its relatives, it became clear that a thorough resampling and molecular analysis of cascade-dwelling frogs of Sumatra was necessary. Herein, we present our analyses of newly sampled material of *C. crassiovis*. The objectives of this study were: 1) to examine the phylogenetic relationships and taxonomic status of *C. crassiovis* and morphologically similar taxa based on new molecular data; 2) to evaluate the phylogenetic position and taxonomy of material topotypic with *C. kampeni*; 3) to assess material from extensive sampling along the longitudinal axis of Sumatra in an effort to elucidate the diversity and distribution of this group of frogs; 4) to assign samples of collected gastromyzophorous tadpoles to specific species based on molecular evidence.

Materials and methods

Sampling strategy

We conducted rapid biological sampling (Ribeiro-Junior et al. 2008) at sites across Sumatra between 2013–2016. All specimens examined were collected during these sampling activities, and additional specimens were collected during 2008 and 2012 (Fig. 1). Rapid sampling entails visiting many sites but with limited time at each site in order to gather as much data as possible from as many sites as possible. This approach is cost effective and indispensable for sampling potentially cryptic species (Ribeiro-Junior et al. 2008). We collected frogs that were morphologically similar to *Chalcorana crassiovis* at their torrential stream habitats along with any gastromyzophorous tadpoles found in the same streams. The sampling included specimens from the reported type locality of the enigmatic taxon *C. kampeni*. Its type locality, when originally described as *Rana pantherina* van Kampen, 1910 was Bandar Baru, a village in the Kabupaten Deli Serdang, Provinsi Sumatera Utara. We collected stream frogs that are morphologically similar to *C. crassiovis* from the hillside streams of Bandar Baru and consider our materials (Appendix 1) topotypic to the original types of *C. kampeni*. The type locality of *C. crassiovis* is "Korinchi, Sumatra, 4,000 feet" (Boulenger 1920). Today, the modern spelling, "Kerinci" is applied to Mt. Kerinci as well as the Kabupaten Kerinci area; the original description does not provide hints as to where exactly the type specimens were collected from within that area. We visited Mt. Ker-

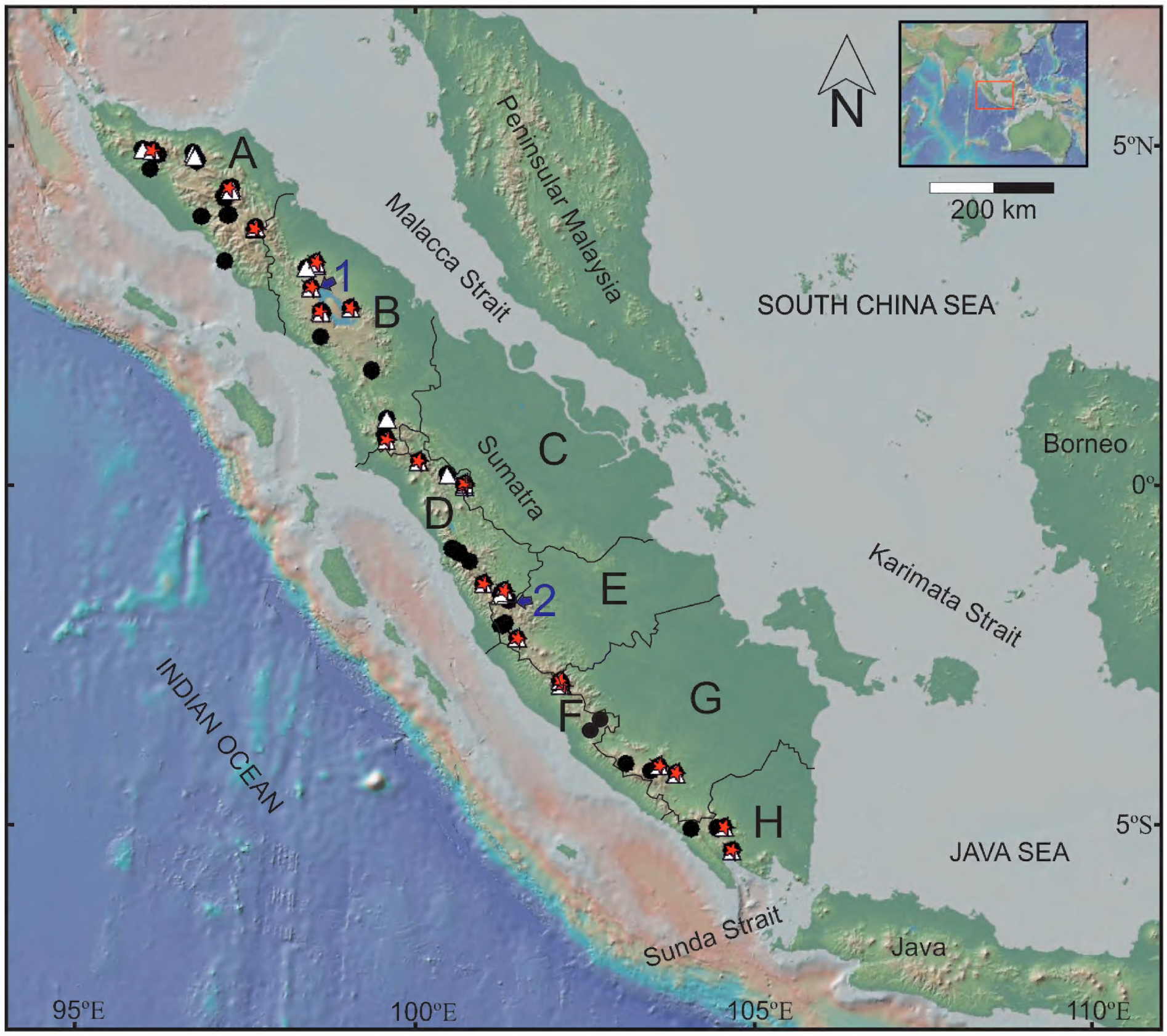

Figure 1. Sampling localities of adult and larva of *Chalcorana crassiovis* specimens for this study. Black circles represent localities of specimens which were examined. White triangles represent localities of specimens which were examined and measured. Red stars represent localities of specimens which were examined, measured, and sequenced. Type locality of *C. kampeni* shown by number 1 (Bandar Baru), number 2 (Kerinci) for *C. crassiovis*. Provinces are shown by alphabet: **A** Aceh, **B** Sumatera Utara, **C** Riau, **D** Sumatera Barat, **E** Jambi, **F** Bengkulu, **G** Sumatera Selatan, **H** Lampung. Borders between provinces are represented by black lines. The map was prepared using GeoMapApp (Ryan et al. 2009).

inci but could not find frogs of the group in question, so our nearest samplings were approximately 10 km north and northeast of Mt. Kerinci and several localities were still within the Kabupaten Kerinci area (Appendix 1).

We followed the general legal guidelines of Germany (Tierschutzgesetz, https://www.gesetze-im-internet.de/tierschg/BJNR012770972.html) for handling and euthanizing the specimens. Each frog was anesthetized slowly and ultimately euthanized in an aqueous solution of chlorobuthanol. Tissue samples of muscle or liver tissue were preserved in either ethanol (96%), RNA later (Sigma Aldrich, USA) or Lysis buffer (0.5 M Tris / 0.25% EDTA / 2.5% SDS, pH 8.2) for DNA analyses. Specimens were fixed in 4% neutral-buffered formalin and then transferred to 70% ethanol for long term storage. All specimens examined in this study are deposited at one of these following museum: The Natural History Museum (**BMNH**), London, United Kingdom; the Museum Zoologicum Bogoriense (**MZB**), Bogor, Indonesia; the Zoologisches Museum Hamburg (**ZMH**), Hamburg, Germany; the Museum of the University of Texas Arlington (**UTA**), Arlington, USA; and the Museum of Vertebrate Zoology (**MVZ**), Berkeley, USA.

In order to uncover the true diversity of *Chalcorana crassiovis,* we acquired DNA sequences from tissue samples of adults (n = 20) from 19 localities across Sumatra. We selected the 20 specimens after a preliminary assessment of the qualitative morphological features of all specimens (n = 329) that were examined. Additionally, we included a subsample of four Sumatran gastromyzophorous tadpoles in the genetic analysis for identification. We

followed the results of previously published studies (Yang 1991, Frost et al. 2006, Oliver et al. 2015) to select potentially related species to compose a diverse and sufficiently comprehensive ingroup in order to test the phylogenetic relationships of our *C. crassiovis* samples. *Staurois* was chosen as the outgroup taxon (Pyron and Wiens 2011). We selected sequence data of *C. chalconota* (Schlegel, 1837), *C. megalonesa* (Inger, Stuart & Iskandar, 2009), *Hydrophylax malabaricus* (Tschudi, 1838), *Hydr. leptoglossa* (Cope, 1868), *Hylarana erythraea* (Schlegel, 1837), *Hyl. macrodactyla* Günther, 1858, *Clinotarsus alticola* (Boulenger, 1882), *Cli. penelope* Grosjean, Bordoloi, Chuaynkern, Chakravarty & Ohler, 2015, and *Staurois guttatus* (Günther, 1858), particularly to serve as generotypic representatives. We applied the name *Cli. penelope* for one sample that was originally loaned under the name *Cli. alticola* (FMNH 268338), because it was identical with available sequences (16S) of *Cli. penelope* (Genbank accession numbers KR827723 [MNHN 2000.4633] and KR827724 [MNHN 930P]; Grosjean et al. 2015).

We added DNA sequences of *Amolops afghanus* (Günther, 1858), *A. indoburmanensis* Dever, Fuiten, Konu & Wilkinson, 2012, *A. marmoratus* (Blyth, 1855), *A. panhai* Matsui & Nabhitabhata, 2006, *Huia sumatrana* Yang, 1991, *H. cavitympanum* (Boulenger, 1893), *H. masonii* (Boulenger, 1884), *H. melasma* Stuart & Chan-ard, 2005, *Meristogenys jerboa* (Günther, 1872) and *M. kinabaluensis* (Inger, 1966) because these taxa have reliably recognizable gastromyzophorous larvae. Finally, we included *Odorrana hosii* (Boulenger, 1891) and *O. livida* (Blyth, 1856) as additional species. *Odorrana hosii* lives syntopically in the same streams with *C. crassiovis*. Sequences of *M. jerboa*, *C. megalonesa, Hyl. macrodactyla, Hydr. malabaricus, Hydr. leptoglossa,* and *O. livida* were obtained from Genbank. The remaining ingroup sequences were generated by this project. The list of voucher specimens (n = 46) comprising the genetic data set is provided in Suppl. material 1.

Laboratory protocols

We extracted DNA from tissue samples (liver, muscle) using Crystal DNA mini Kit (Biolab), PeqGOLD Tissue Kit (Peqlab), or Qiagen DNeasy Blood and Tissue Kit. We then amplified mitochondrial genes (12S rRNA, 16S rRNA, and $tRNA^{val}$) and nuclear genes (recombination-activating gene 1, RAG1, tyrosinase exon 1, TYR) for all frog samples. For tadpoles, we sequenced the 12S rRNA and 16S rRNA (which include $tRNA^{val}$) genes as barcode tool to associate them with adults. Primer information and PCR annealing temperatures applied for this study are provided in Table 1. We cleaned the PCR products using ExoSAP-IT™ and let a contractor (Macrogen, LGC, or Microsynth) sequenced the purified forward and reverse strands. We used GENEIOUS v 8.0 (Kearse et al. 2012, Biomatters Inc., www.geneious.com) to check sequence quality of both strands by comparison to their respective chromatograms, and to assemble and edit if necessary. Furthermore, we aligned sequences for each gene loci using MAFFT v7.017 (Katoh and Standley 2013, module implemented in GENEIOUS v 8.0) with default setting. We eliminated poorly aligned positions and divergent regions of an alignment of each DNA loci using GBLOCK 0.91b (Castresana 2000, Talavera and Castresana 2007) which included in the online software http://www.phylogeny.fr (Dereeper et al. 2008), with setting for a less stringent selection (allows smaller final block and allows gap positions within the final block).

Phylogenetic analyses

We ran PARTITION FINDER v.1.1 (Lanfear et al. 2012) on our concatenated dataset using Bayesian Information Criterion (BIC) to find the best models by testing a variety of models and partitioning strategies for each loci. Four partitions were proposed by the analysis: 12S rRNA, 16S rRNA, and $tRNA^{val}$: GTR+I+ G; RAG1 codon 1, RAG1 codon 2, and TYR codon 1: HKY+I; RAG1 codon 3: HKY+ G; TYR codon 3: K80+G. We then employed Maximum Likelihood (ML) and Bayesian Inference (BI) to infer phylogenetic trees. To explore partitions, we constructed trees using individual loci, concatenated sequences for mitochondrial loci only, concatenated sequences for nuclear loci only, and concatenated sequences for combined mitochondrial and nuclear loci; the later was used for optimal tree reconstruction (Kluge 1989, 2004). ML tree search included 1000 bootstrap replicates in RAXML v. 8 (Stamatakis 2014) and was performed using the CIPRES Science Gateway V 3.3 (Miller et al. 2010, www.phylo.org/sub.sections/portal), with default parameters. We also used the CIPRES Science Gateway to find optimal phylogenetic trees with MR. BAYES v 3.2.6 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) in two independent runs, each with four chains, and running for 50 million generations with sampling every 1000 generations. Convergence was assessed by examining all parameters and the effective sample sizes in TRACER v.1.6 (Rambaut et al. 2014) after discarding the first 25% of samples as burn in. We viewed trees that resulted from RAXML and MR. BAYES in FIGTREE v.1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/) and prepared the tree in Fig. 2 using CORELDRAW X6. Nodal support with Bootstrap values (BS) $\geq$ 70 for ML tree (Hillis and Bull 1993) and Posterior Probability value (PP) $\geq$ 0.95 for Bayesian analyses (Huelsenbeck and Ronquist 2001) are herein considered as strong support (Huelsenbeck and Ranala 2004, Mulcahy et al. 2011). We also calculated genetic *p*-distances using MEGA 7.0.25 (Kumar et al. 2016) from 16S ribosomal subunit.

Adult and tadpole morphology

We measured a total of 175 adult *Chalcorana crassiovis* group frogs (males = 133, females = 42). These represent a subsample of all specimens examined (n = 329, Appendix 1). Measurements were taken with digital calipers with 0.01 mm reading accuracy. The subsample of 175 specimens included the sequenced specimens (except for MVZ271526, tissue only). Measurements were taken by UA, following current standards for morphological mea-

Table 1. Gene markers, primer sequences, annealing temperatures and sequence length information.

Markers	Sequence	Annealing temp (°C)	Length (bps)	Citation
12S	12SZ-L: AAAGGTTTGGTCCTAGCCTT 12SK-H: TCCRGTAYRCTTACCDTGTTACGA	52	825	Goebel et al. (1999)
16S+ tRNA^{val}	12sm: GGCAAGTCGTAACATGGTAAG 16sd: CTCCGGTCTGAACTCAGATCACGTAG	51	1406	Pauly et al. (2004), Oliver et al. (2015)
RAG1	Rag1 1F: GCMTTGCTSCCRGGGTATCA Rag1 2R: TCAATGGACGGAAGGGTTTCAATAA	50	801	Oliver et al. (2015)
TYR	Tyr1A: AGGTCCTCTTRAGCAAGGAATG Tyr1G: TGCTGGGCRTCTCTCCARTCCCA	57	579	Oliver et al. (2015)

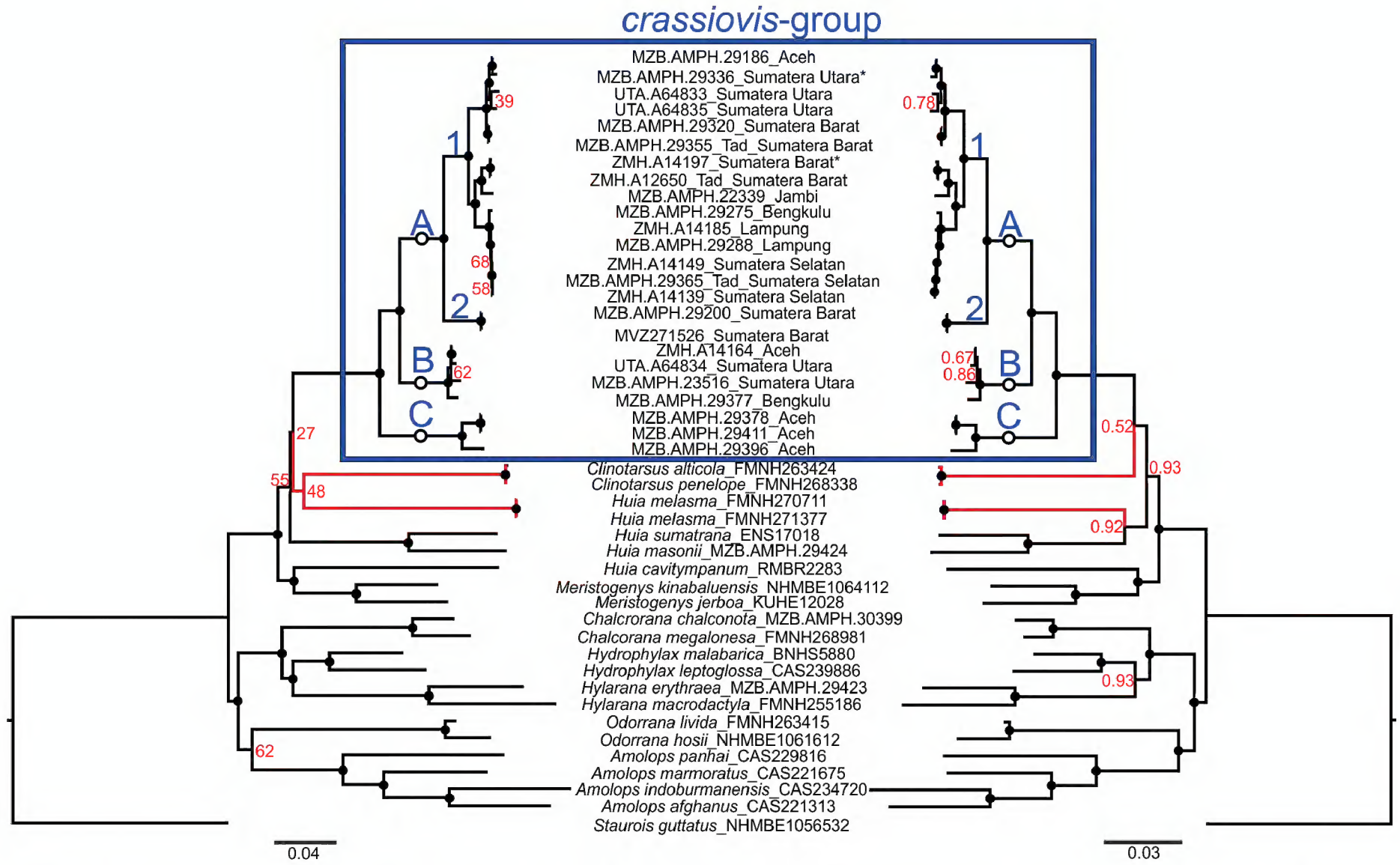

Figure 2. Bayesian (on the right) and Maximum Likelihood (on the left) trees showing the phylogenetic relationship of the *crassiovis*-group. **A, B, C** are distinct lineages within *crassiovis*-group. Black circles represent well supported nodes (PP ≥ 0.95 and BS ≥ 70). Red branches represent relationship between *Clinotarsus* and *Huia melasma*. Tadpole sequences named with specimen number_Tad_locality (province). Adult sequences named with specimen number_locality (province). MZB.AMPH.29336 and ZMH.A14197 were collected from the type locality of *C. kampeni* and *C. crassiovis*, respectively.

surements of frogs (e.g., Matsui et al. 2010, Shimada et al. 2011, Waser et al. 2016, and Watters et al. 2016). All acronyms and definitions of measured distances are explained in Table 2 and illustrated in Suppl. material 2A. We determined sex by the presence of nuptial pads and vocal sacs in males, and their absence and presence of eggs, respectively, in females. We analyzed sexes separately to control for bias resulting from sexual dimorphism.

We collected tadpoles from rocks in fast flowing water using a fishnet and followed the procedures suggested in Haas and Das (2011). We preserved tail tissues of the photographed specimens in either 96% ethanol or RNAlater. We fixed and stored the remaining specimens from the series in neutral-buffered formalin solution (4%). We staged the tadpoles (n = 29) according to the table in Gosner (1960). The range of Grosner stages was 25–42, with the majority of specimens at Stage 25 (n = 12). We assigned the 25 tadpoles that were not sequenced to the respective clade of the genetically examined tadpoles based on their morphological similarity. Standard measurements for tadpoles (Altig 2007, Shimada et al. 2007, Haas and Das 2011, Oberhummer et al. 2014) were taken from digital images with a calibrated digital microscope VHX5000 KEYENCE Corporation, Japan (Table 3 and Suppl. material 2B) by UA. We slightly edited all images in this study using Adobe PHOTOSHOP CS6 (contrast adjustment, background, cleanup, cropping, sharpening). We prepared image plates with CORELDRAW X6.

We followed the morphological terminology of Duellman (2001) and Kok and Kalamandeen (2008). For webbing we used the formula in Guayasamin et al. (2006). We adopted the suggestions for glands cluster definitions from Shimada et al. (2015).

Table 2. Standard measurement for adult specimens used in this study. See Suppl. materials 2A for illustration.

Acronym	Characters	Explanation
SVL	Snout Vent Length	From tip of snout to vent
HL	Head Length	From tip of snout to angle of jaw
HW	Head Width	Maximum width of the head at angle of jaw
SL	Snout Length	From tip of snout to the anterior corner of eye
SN	Snout Narial distance	From tip of snout to center of nares
ED	Eye Diameter	Maximum distance between anterior and posterior corners of eye
EN	Eye Narial distance	From center of naris to anterior circumference of eye
IND	Internarial Distance	Distance between centers of nares
IOD	Interorbital Distance	Minimum distance between upper eyelids
UEW	Upper Eyelid Width	Maximum transverse width of upper eyelid
TYv	vertical Tympanum diameter	Maximum vertical diameter, from the outer edges of tympanic annulus
TYh	horizontal Tympanum diameter	Maximum horizontal diameter, from the outer edges of tympanic annulus
ET	Eye-Tympanum distance	From posterior corner of eye to the anterior edge of tympanum
LAL	Lower Arm Length	From the tip of the elbow to the proximal edge of the palmar tubercle
HAL	Hand Length	From the proximal edge of the palmar tubercle to the tip of Finger III
FE	Femur Length	From center of vent to lateral of knee
TL	Tibia Length	Distance between anterior point of knee and posterior surface of heel with both tibia and tarsus flexed
FL	Foot Length	From proximal end of inner metatarsal tubercle to tip of Toe IV
IMTL	Inner Metatarsal Tubercle Length	Maximum distance between anterior and posterior tip of inner metatarsal tubercle
F1L	Finger I Length	From the proximal edge of subarticular tubercle of Finger I to the tip of Finger I
F2L	Finger II Length	From the proximal edge of subarticular tubercle of Finger II to the tip of Finger II
F3DW	Finger III Disc Width	Maximum width of Finger III disc
T4DW	Toe IV Disc Width	Maximum width of Toe IV disc

Table 3. Standard measurement for tadpole specimens used in this study. See Suppl. materials 2B for illustration.

Acronym	Character	Explanation
BL	Body Length	From snout to the point where the axis of the tail (horizontal septum of myotomes) meets the body wall
BH	Body Height	Maximum body height at trunk
BW	Body Width	Maximum body width
EN	Eye Narial distance	From center of eye to the center of naris
ED	Eye Diameter	Diameter of eye measured horizontally
ES	Eye Snout distance	From tip of snout to the anterior circumference of the eye
IND	Inter Narial Distance	Distance between center of nares
IOD	Inter Orbital Distance	Minimum distance between eyeballs
LFH	Lower Fin Height	Measured at point of maximum tail height
MTH	Maximum Tail Height	Measured from the maximum point of upper fin to the maximum point of lower fin
NL	Narial Length	Maximum aperture of narial opening in dorsal view
ODW	Oral Disc Width	Maximum width of oral disc
SN	Snout Narial distance	From snout to the center of naris
SS	Snout Spiracle distance	From snout to end of spiracle tube
SUL	Sucker Length	From anterior end to posterior end of abdominal sucker
SUW	Sucker Width	Maximum width of abdominal sucker
SSL	Snout and Sucker Length	From the tip of snout and to posterior end of abdominal sucker
TTL	Total Length	From tip of snout to tip of the tail
TAL	Tail Length	Calculated as: Total Lenght (TTL) – Body Length (BL)
TMH	Tail Muscle Height	Maximum tail muscle height at body-tail junction
TMW	Tail Muscle Width	Maximum tail muscle width at body-tail junction
UFH	Upper Fin Height	Measured at point of maximum tail height

Results and discussion

Phylogenetic analyses and morphology

We inferred optimal phylogenetic trees from our concatenated dataset (3611 bps) comprising all gene markers (12S rRNA+16S rRNA+tRNA^{val}+RAG1+TYR), of which 12.16% gaps and undetermined characters state. The best log likelihood of ML tree was -25426.240268.

The tree topologies recovered from ML and BI, respectively, were identical, except for the arrangement of *Clinotarsus* and *Huia melasma* (Fig. 2). Our BI tree (Fig. 2 right) suggested *Clinotarsus* to be sister taxon of the *Chalcorana crassiovis* group and *H. melasma* to be the sister taxon of *H. sumatrana*+*H. masonii*. In the ML tree (Fig. 2 left), however, *Clinotarsus*+*H. melasma* and the *C. crassiovis* group were sister taxa. Based on a dataset of two nuclear markers (RAG1+TYR) and lacking *C. crassiovis*, Stuart (2008) suggested *Clinotarsus*+*H. melasma* to be the sister taxon of a clade comprising other *Huia* species from Sumatra, Java, and Borneo, and *Meristogenys*. In contrast, based on a larger dataset, Pyron and Wiens (2011) identified *Clinotarsus* as sister taxon to *H. sumatrana*+*H. masonii*, whereas *H. melasma* was sister taxon to all other species in a clade comprising *Huia*+*Meristogenys*+*Clinotarsus*. However, all of these scenarios for the arrangement of *Clinotarsus* and *H. melasma* within ranid phylogeny had low nodal support. Consequently, we prefer not to draw any phylogenetic conclusions or recommend taxonomic amendments concerning *Clinotarsus* or *H. melasma*.

With the exception of the incongruence in the position of *Clinotarsus* and *Huia melasma*, both the ML and BI trees confirmed the existence of two major clades each with strong nodal support (Fig. 2): *crassiovis*-group+*Huia*+*Meristogenys*+*Clinotarsus* (PP = 1; BS = 100) and *Amolops*+*Odorrana*+*Hylarana*+*Hydrophylax*+*Chalcorana* (PP = 0.97; BS = 75). This result strongly suggests that *C. crassiovis* is not the closest relative of either *C. chalconota* (generotype) or *C. megalonesa*. DNA barcoding (12S rRNA+16S rRNA+tRNA^{val} genes) successfully matched samples of gastromyzophorous tadpoles to adult in the *crassiovis*-group.

Our results further corroborate previous studies (Stuart 2008, Pyron and Wiens 2011) in that the genus *Huia* is paraphyletic in its current composition. Yet, our phylogenetic trees were different from these previous studies concerning other genera. For example, our trees suggest *Odorrana* to be more closely related to *Amolops* (PP = 0.98, BS = 62, Fig. 2) than to *Chalcorana*+*Hylarana*+*Hydrophylax*. Stuart (2008) and Pyron and Wiens (2011) presented evindence that *Odorrana* was as closely related to some *Rana* or *Lithobathes*, embedded in a more inclusive assemblage (including, among others, *Chalcorana*, *Hylarana*, and *Hydrophylax*, in current generic assignment). To corroborate that was beyond the scope of our analysis and, thus, we did not include samples of *Rana* and *Lithobates*.

Within the clade of the *crassiovis*-group (Fig. 2), unexpected genetic diversity was revealed along the Sumatran transect. Our phylogenetic tree showed three distinct, well supported clades within our samples that previously would have been all be assigned to *Chalcorana crassiovis,* i.e., *Clade* A, Clade B, and Clade C (PP = 1, BS = 100). These three clades showed high genetic divergence among each other (Clade A–B: 6.61–8.53%, Clade A–C: 7.46–9.59%, and Clade B–C: 7.74–8.74%, respectively, Suppl. materials 3). Clade A comprises frogs from northern part of Provinsi Aceh to the southern part of Provinsi Lampung, including samples from the type localities of *C. crassiovis* (ZMH.A14197) and of *C. kampeni* (MZB. AMPH.29336), respectively. We found no evidence, that specimens from the type locality of *C. kampeni* were significantly divergent genetically from the remaining lineages in Clade A (uncorrected *p*-distance = 2.56%). Clade B encompass samples from Aceh, Sumatera Utara, and Bengkulu provinces, whereas Clade C consists of samples from the northern part of Provinsi Aceh. Apart from clearly being genetically distinct, we also found morphological features distinguishing both Clades B and Clade C, respectively, from Clade A. The morphology of our specimens in Clade A, however, fit well the description of *C. crassiovis* (*sensu* Inger and Iskandar 2005 assuming synonymy with *C. kampeni*). In the expanded morphological dataset, both quantitative data (morphometric values and body ratio values) and qualitative data (e.g., skin texture and coloration, iris coloration, pattern of rear of thigh, see Fig. 3) clearly clustered the *C. crassiovis* specimens and their respective geographic division into Clades A–C. Morphological analyses are detailed in the taxonomic section below.

Frogs in Clade A share a similar elevational range (425–1545 m a.s.l.) and a similar habitat type (primary forest or good secondary forest) with Clade C (314–1000 m a.s.l.). Clade A also overlaps in elevational range with Clade B (1190–2033 m a.s.l.). In Aceh, we observed specimens of Clade A and Clade B at the same stream (1190 m a.s.l.), as well as frogs of Clade A and Clade C in another stream (1000 m a.s.l.). These observations suggest independent evolution occurring with the syntopic species. Two genetic samples (MZB.AMPH.29200 and MVZ271526) from Cagar Alam (=Nature Reserve) Rimbo Panti, Kecamatan (=District) Panti, Kabupaten (=Regency) Pasaman, Provinsi (=Province) Sumatera Barat, were separated by 4.05–4.90% uncorrected *p*-distance from their nearest relatives (Suppl. materials 3) and were sister to all other samples in Clade A (Fig. 2). Although this could be indicative of a separately evolving lineage, we could not find unambiguous morphological evidence that could separate these two with certainty from that of the remaining samples in Clade A. Some morphological features in the Rimbo Panti specimens, such as rear of thigh pattern and webbing formula (Fig. 4) overlap with other populations in Clade A. Rimbo Panti specimens (n males = 9, n females = 3) are bigger in size (SVL males = 46.45–48.87 mm, females = 78.00–83.99 mm) com-

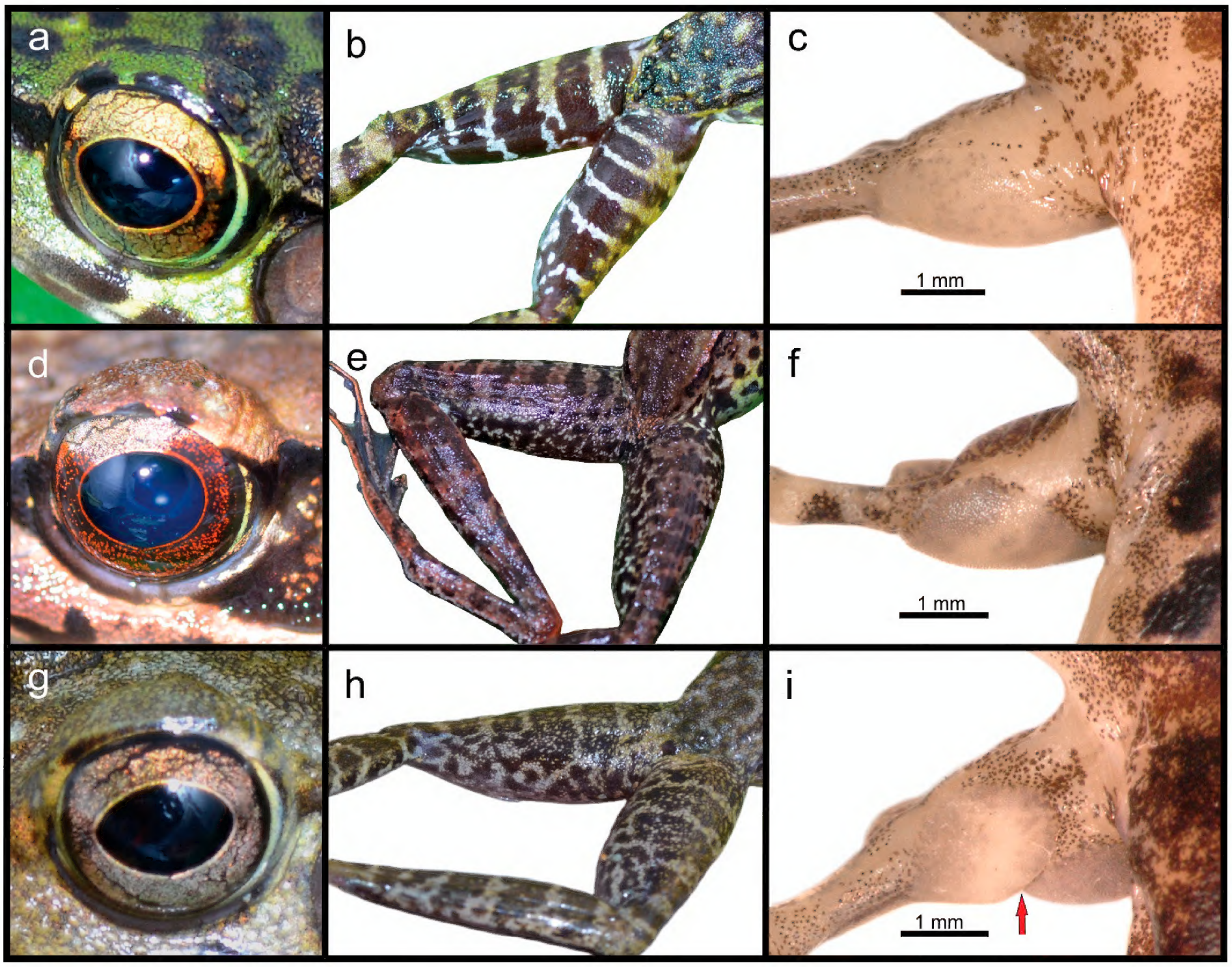

Figure 3. Comparison of three lineages within Clade 1 based on the coloration of iris, the coloration of rear of thigh, and nuptial pad. Clade 1A (**a–c**), Clade 1B (**c–d**) and Clade 1C (**g–i**). Photographs were taken from ZMH.A14197, male, Provinsi Sumatera Barat (**a–c**); ZMH.A14194, female, Provinsi Bengkulu (**d–e**); MZB.AMPH.23524, male, Provinsi Sumatera Utara (**f**); and MZB.AMPH.29396, male, Provinsi Aceh (**g–i**). Photos by U. Arifin.

pared to the remaining samples of this clade (SVL males = 30.30–41.75 mm, females = 40.98–77.73 mm). However, the specimens of Rimbo Panti were collected at 450 m a.s.l. whereas the smallest body size of the remaining specimens of Clade A were from 1355 m a.s.l. at Gunung Kunyit, Kabupaten Kerinci, Provinsi Jambi (SVL males = 30.03–32.81 mm). The rear of thigh of Rimbo Panti specimens is typically mottled, light on dark background (Fig. 4d). The mottling pattern varied among specimens and some specimens are similar in pattern to the specimens from other regions in Clade A. The majority of specimens in Clade A were fully webbed, except for one free phalanx on Toe IV. Six specimens from Rimbo Panti were fully webbed, and six (all males) had webbing only reaching the base of the disc of Toe IV but deeply incised). This webbing pattern is also present in other specimens in Clade A. At present we conservatively consider these differences as interspecific variation, despite the genetic distance.

Three of the four tadpoles sequenced belonged to Clade A and one tadpole belonged to Clade C. Morphological characters such as shape of the jaw sheath and number of keratodont rows showed distinct separation Clades A and C (see below) and were in accordance with the genetically justified assignment.

Taxonomic Amendments: Genus and Species Descriptions

Herein we adopt the Unified Species Concept (de Queiroz 2005) and consider Clades A–C as independently evolving units. Evidence for this assumption is provided by substantial genetic divergence (6.61–9.59%, Suppl. materials 3), robustly supported reciprocal monophyly in phylogenetic analyses, adult and tadpole morphology, geographical distribution, and syntopic occurence. We believe that the establishment of a new genus for the *crassiovis*-group is in place because 1) the group is monophyletic; 2) the group is biogeographically well delimited (endemic to Sumatra); 3) the branch length (Fig. 2) that separates the *crassiovis*-group from any potential relative is substantial and on par with nodes that define other genera in ranids, indicating similar ages of origin. The new genus is comprised of three species, two of which are new to science (Fig. 2).

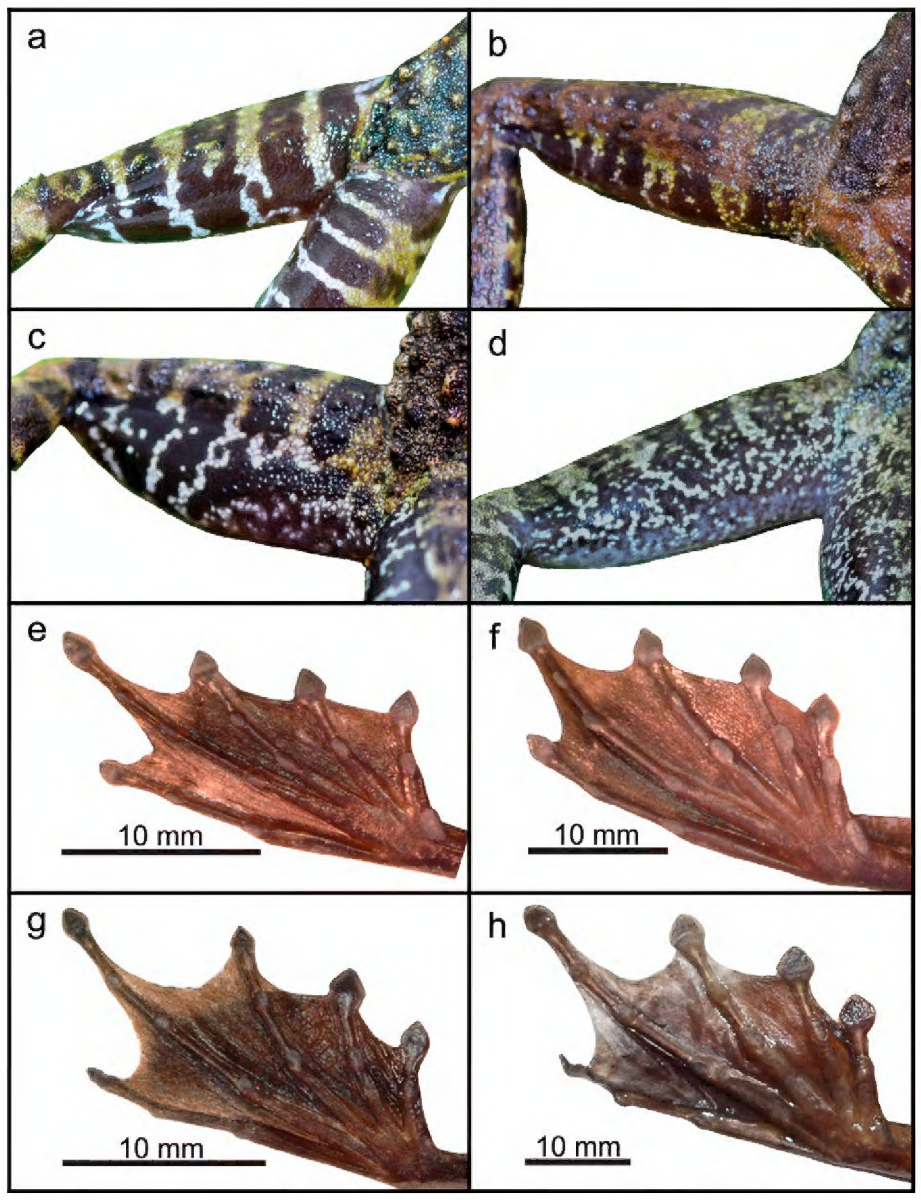

Figure 4. Variation of rear of thigh pattern and webbing on toes of the specimens within Clade 1A. Photographs were taken from ZMH. A14197, male, Provinsi Sumatera Barat (**a, g**); MZB.AMPH.29196, female, Provinsi Aceh (**b**); MZB.AMPH.29320, male, Provinsi Sumatera Barat (**c**); MZB.AMPH.29200, male, Provinsi Sumatera Barat (**d–e**); ZMH.A14170, female, Provinsi Sumatera Barat (**f**); ZMH.A14185, female, Provinsi Lampung (**h**). Photos by U. Arifin

Sumaterana gen. n.

http://zoobank.org/1BC968B1-5D37-4D67-9413-8A4FA811DC83

Fig. 5a–c

Type species. *Rana crassiovis* Boulenger, 1920, Syntypes: two adult females, BMNH1947.2.3.99 and BMNH1947.2.4.1.

Diagnosis. *Sumaterana* gen. n. belongs to a group of ranid torrent frogs, along with *Huia* and *Meristogenys* that possess gastromyzophorous larvae (Inger 1966, Inger and Gritis 1983, Inger 1986, Yang 1991). *Sumaterana* gen. n. species can be diagnosed by a combination of: (1) gastromyzophorous tadpole; (2) larval upper jaw sheaths thick, smooth, broadly arched, with thinner medial section; (3) lower jaw sheaths undivided, smooth, and V-shaped; (4) Labial Tooth Row Formula (LTRF): 8(5–9)/8(1) to 9(5–9)/9(1); (5) infraorbital and postorbital gland clusters present; (6) adult frogs medium sized (SVL males = 27.94–48.87 mm; females = 40.98–83.99 mm); (7) dorsum finely granulated, with or without scattered tubercles; (8) supratympanic fold present (skin fold above the tympanum, starting behind the eye); (9) posttympanic fold absent (vertical skin fold immediately posterior to tympanum); (10) dorsolateral fold absent or present; (11) tibia length 58.08–79.67% SVL; (12) outer metatarsal tubercle absent; (13) inner metatarsal tubercle present; (14) Finger I relatively shorter or subequal to Finger II; (15) width of finger discs larger or subequal to width of toe discs; (16) vocal sacs and nuptial pads present; (17) humeral gland absent.

Comparison. *Sumaterana* gen. n., *Huia*, *Meristogenys*, and *Amolops* can be distinguish from *Chalcorana*, *Clinotarsus*, *Hydrophylax*, *Hylarana*, *Odorrana*, and all other ranids (except, *Rana sauteri*, Kuramoto et al. 1984) by having gastromyzophorous tadpoles. Although *R. sauteri* has gastromyzophorous tadpoles (Kuramoto et al. 1984), Gan et al. (2015) pointed out that *R. sauteri* larvae differs from the gastromyzophorous tadpole of *Huia* and *Meristogenys* in significant features of the sucker (see below). *Amolops* and *R. sauteri* seem only distantly related to *Huia* and *Meristogenys* (Pyron and Wiens 2011; this study), and independent evolution in gastromyzophorous tadpoles must be assumed. We corroborate and expand the conclusion of Manthey and Denzer (2014) that the tadpoles of *Sumaterana* gen. n., *Amolops*, *Huia*, and *Meristogenys* can be distinguished by the shape of their jaw sheaths. The jaw sheath of *Sumaterana* gen. n. is characterized by (followed by *Amolops*; *Huia*; *Meristogenys* features in parantheses): the upper jaw sheath thick, broadly arched, with thinner medial section (thick, broadly arched, without the medial thinning; M-shaped or ∧-shaped; divided; Yang 1991, Manthey and Denzer 2014); lower jaw sheath V-shaped (V-shaped; V-shaped; divided or undivided; Yang 1991, Manthey and Denzer 2014). The number of keratodont rows on the lower lip is eight to nine in *Sumaterana* gen. n. (three to five rows in *Amolops*, except for *A. cremnobatus* with six rows (Inger and Kottelat 1998); six rows or more in *Huia* (Manthey and Denzer 2014); four rows or more in *Meristogenys* (Inger and Stuebing 2009, Manthey and Denzer 2014, Shimada et al. 2015). *Sumaterana* gen. n. has two glandular clusters, infraorbital and postorbital (postorbital and abdominal clusters in *Amolops* (Yang 1991, Inger and Kottelat 1998, Liu et al. 2000, Matsui and Nabhitabhata 2006, Ngo et al. 2006), except for *A. cremnobatus*, postorbital and midlateral clusters (Inger and Kottelat 1998); a combination of infraorbital, postorbital, prespiracular, midlateral, and variably caudal/fin clusters in *Meristogenys* (e.g., Yang 1991, Matsui et al. 2010, Shimada et al. 2011, Shimada et al. 2015); and a combination of caudal/fin, postorbital, midlateral, and infraorbital clusters in *Huia* (Yang 1991; UA pers. observ.).

Adult *Sumaterana* gen. n. can be distinguished from *Huia, Meristogenys,* and *Amolops* by: lacking posttympanic fold (present in *Huia, Meristogenys* and *Amolops*; Yang1991; UA unpubl. data); the disc of Finger III wider or almost equal to that of Toe IV (subequal in *Huia*, less or equal to in *Meristogenys*, wider in *Amolops*; Yang 1991); Finger I length shorter or subequal to that of Finger II (Finger I ≥ Finger II in *Huia*, Finger I > Finger II in *Meristogenys*, Finger I ≤ Finger II in *Amolops*; Yang 1991); lacking an outer metatarsal tubercle (present in *Huia* except for

Figure 5. *Sumaterana* gen. n. species: (**a**) *S. crassiovis* comb. n., ZMH.A14197, male, Provinsi Sumatera Barat; (**b**) *S. dabulescens* sp. n., MZB.AMPH.29396, male, holotype, Provinsi Aceh; (**c**) *S. montana* sp. n., ZMH.A14194, female, paratype, Provinsi Bengkulu. Photos by U. Arifin.

H. cavitympanum, present in *Meristogenys* except for *M. kinabaluensis*; Yang 1991); tibia length relative to SVL 58.08–78.39% (> 70% in *Huia* and in *Meristogenys*; Yang 1991); furthermore, *Sumaterana* gen. n. differs from *Huia* by having a translucent but non-transparent tympanum; tympanum not encased by dark Π-shaped marking (Manthey and Denzer 2014); and dorsolateral folds less distinct or absent. *Sumaterana* gen. n. differs from *Amolops* by having diamond-shaped finger and toe tips (rounded in *Amolops*) and relatively smaller fingers and toe discs.

Etymology. *Sumaterana* is a compound generic epithet created from the Indonesian proper noun Sumatera, the Indonesian name for the island of Sumatra, and *rana*, the feminin Latin word for frog. Sumatera itself is named after the kingdom of Samudra Pasai, which was located along the coast of Aceh, Sumatra from the 13th to the 16th centuries CE. Samudra is a sanskrit word that means gathering of the seas, a place where the Andaman, Java, and South China seas meet the Indian Ocean. *Rana*, was also the very first generic name to be assigned to a member of the *S. crassiovis* group, endemic to the island of Sumatra.

Common name. Sumatran Cascade Frogs (English) and Katak Jeram Sumatra (Bahasa Indonesia).

Phylogenetic definition and content. *Sumaterana* gen. n. is a node-based genus that consists of three known species: *Sumaterana crassiovis* comb. n. (Fig. 2 Clade A, Fig. 5a), *S. montana* sp. n. (Fig. 2 Clade B, Fig. 5c), and *S. dabulescens* sp. n. (Fig. 2 Clade C, Fig. 5b), and their most recent common ancestor. *Chalcorana kampeni* is considered a junior synonym of *S. crassiovis* comb. n. based on Inger and Iskandar (2005) and the new molecular evidence. The monophyletic clade of *Sumaterana* gen. n. is restricted to the island of Sumatra, Indonesia. Our phylogenetic analyses and morphological examination supports these taxonomic recognitions (uncorrected *p*-distances in Suppl. materials 3).

Distribution and habitat. Species of *Sumaterana* gen. n. inhabit riparian habitats in primary or secondary forest in Sumatra, Indonesia. Inhabited streams are typically fast flowing, 5 m wide or less, dominated by big rocks (diameter > 1 m). The known elevational range is from 314–2033 m a.s.l.. Adult frogs of these genus usually perched on rocks or vegetation at the stream. Tadpoles of these frogs can be found in groups attached to the top or sides of rocks in fast moving water.

Sumaterana crassiovis comb. n.

Figs 2 Clade A, 5a, 6a

Rana pantherina Van Kampen, 1910.
Rana crassiovis Boulenger, 1920.
Rana (*Hylorana*) *kampeni* Boulenger, 1920.
Rana (*Hylorana*) *crassiovis* Boulenger, 1920.
Rana (*Hylarana*) *kampeni* Van Kampen, 1923.
Rana (*Hylarana*) *crassiovis* Van Kampen, 1923.
Rana (*Chalcorana*) *kampeni* Dubois, 1992.
Rana (*Chalcorana*) *crassiovis* Dubois, 1992.
Hydrophylax kampeni Frost et al., 2006.
Hydrophylax crassiovis Frost et al., 2006.
Hylarana kampeni Che et al., 2007.
Hylarana crassiovis Che et al., 2007.
Chalcorana kampeni Fei et al., 2010; Oliver et al., 2015.
Chalcorana crassiovis Fei et al., 2010; Oliver et al., 2015.

Syntypes. Two adult females (BMNH1947.2.3.99 and BMNH1947.2.4.1-Fig. 7), Kerinci, Sumatra, Indonesia, 4000 feet (~1219 m a.s.l.), coll. Robinson-Kloss Expedition on the Batrachians. Based on the lack of morphological distinguishing characters (Inger and Iskandar 2005) and low genetic divergence (2.56%, Suppl. materials 3) of topotypic specimens (this study), we consider *C. kampeni* a junior synonym of *S. crassiovis* comb. n..

Referred specimens (283). 262 adults (128 of them: 96 males and 32 females; were measured) and 21 tadpoles collected from Aceh up to Lampung (Appendix 1).

Description. Specimens were assigned to *Sumaterana crassiovis* comb. n. based on comparison of material from Kabupaten Kerinci. *Sumaterana crassiovis* comb. n. is described by the following combination of characters: a medium sized species, SVL in males 30.03–48.87 mm,

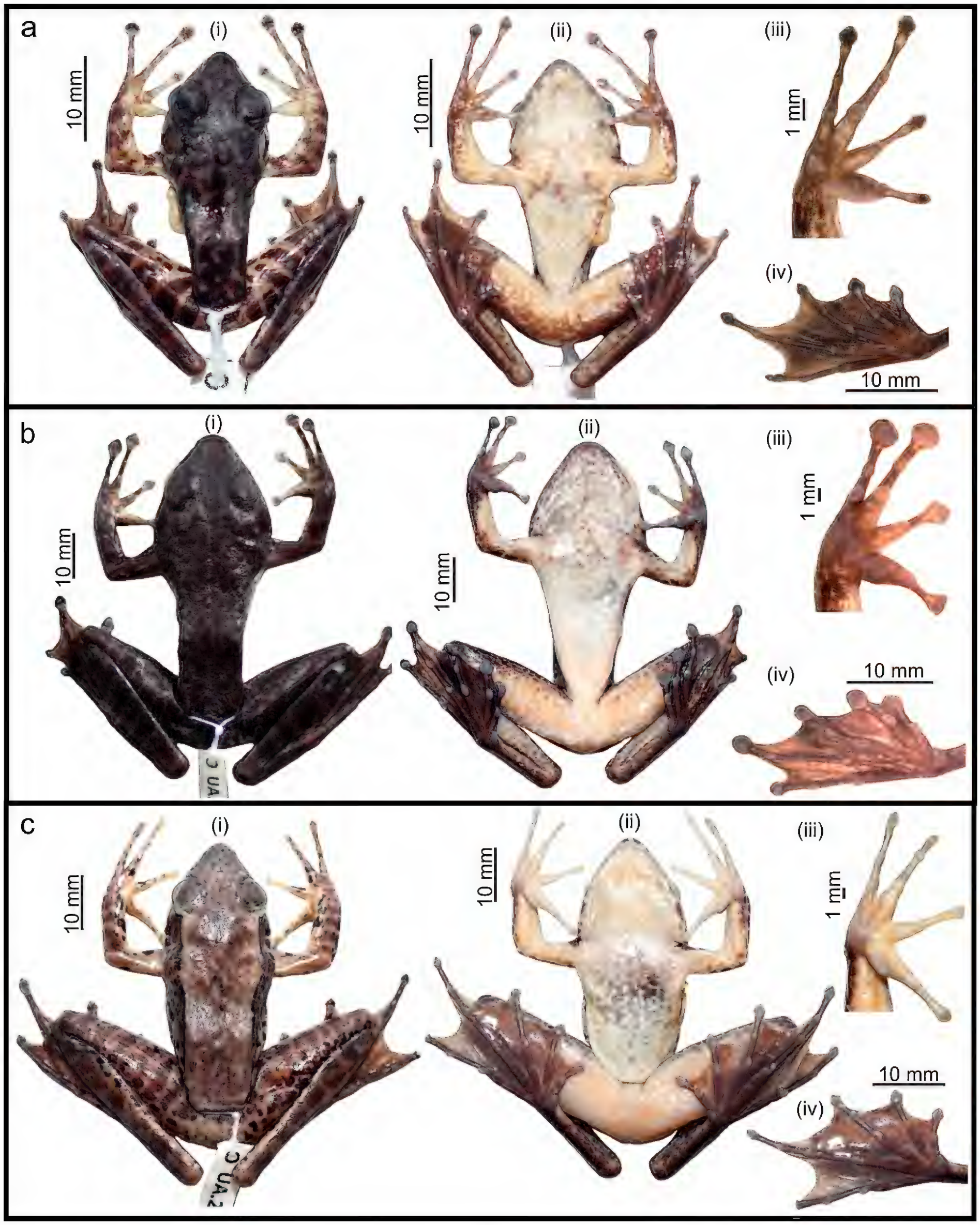

Figure 6. Morphological comparison of (**i**) dorsal, (**ii**) ventral, (**iii**) palmar, and (**iv**) plantar regions of *Sumaterana* gen. n. species. (**a**) *S. crassiovis* comb. n., ZMH.A14197, male, Provinsi Sumatera Barat; (**b**) *S. dabulescens* sp. n., ZMH.A14159, female, paratype, Provinsi Aceh; (**c**) *S. montana* sp. n., ZMH.A14194, female, paratype, Provinsi Bengkulu. Photos by U. Arifin.

females 40.98–83.99 mm; head width subequal to head length; snout rounded, obtusely pointed in dorsal view, slightly protruding in lateral view; nostril closer to snout than to eye; vomerine teeth present, in oblique groups, between choanae; tongue lanceolate; loreal area deeply concave; canthus rostralis sharp, constricted behind nostrils; rictal ridge present; tympanum distinct, translucent (not transparent); interorbital distance 75.96–124.80% width

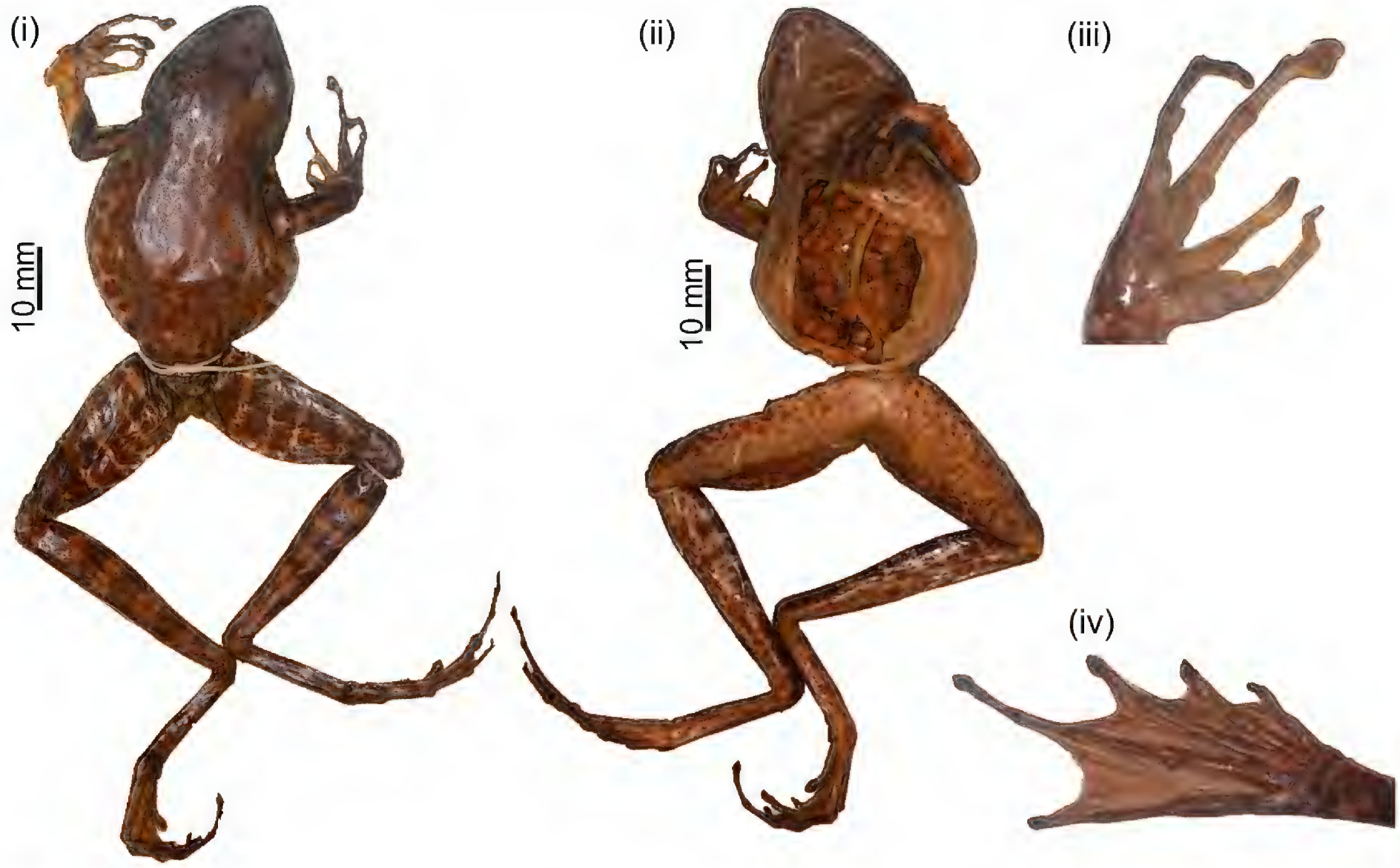

Figure 7. Pictures of dorsal (**i**), ventral (**ii**), palmar (**iii**), and plantar (**iv**) regions of the type species of *Sumaterana crassiovis* comb. n. (BMNH1947.2.4.1, female). Photos by U. Arifin.

of upper eyelid in females, 68.26–120.31% width of upper eyelid in males; pineal spot visible; dorsolateral fold absent; supratympanic fold thick, posttympanic fold absent; dorsum finely granulated with scattered tubercles, variable in size and density; flanks coarsely granulated with few tubercles; venter smooth, granulated posteriorly; rear of thigh usually barred as continuation of thigh dorsal pattern; arm slender, lower arm length 19.03–24.18% SVL in females and 19.58–25.46% SVL in males; hand length 31.54–36.98% SVL in females and 31.77–39.23% SVL in males; fingers long, without webbing; fingertips expanded into discs, diamond-shaped, with circummarginal groove; Finger I < Finger II, Finger III longest; fringes present on the outer phalanges of all fingers; subarticular tubercles distinct; width of Finger III disc > width of Toe IV disc; hindlimbs long, articulation of the heels reaching beyond tip of snout, when limb aligned to body; relative femur length 85.39–94.32% tibia length in females, 85.82–95.02% tibia length in males; length of tibia 60.17–70.52% SVL in females, 58.78–76.44% in males; toes slender and long; tip of toe extended into disc, diamond-shaped, with circummarginal grooves; toe lengths: I < II < III < V < IV, Toe V only slightly longer than Toe III; Toes I, II, III, and V fully webbed, webbing of Toe IV usually one phalanx free ($I(1^{+/-}—1^{+/-})II(1^{+/-}—1^{+/-})III(1^{+/-}—2^{+/-})IV(2^{+/-}—1^{+/-})V$); subarticular tubercles distinct; inner metatarsal tubercle distinct, oval, 92.07–212.77% T4DW in males and 98.80–150.00% in females; outer metatarsal tubercle absent; tarsal fold absent. (Measurements: Tables 4–5).

Coloration. Dorsal skin background green in life, with dark blotches around tubercles, lighter areas on the dorsum forming irregular network pattern; dark line connects the eye and the snout; the upper and lower lips with dark blotches on a light background; iris golden yellow, reddish anteriorly and posteriorly, with a dark netting pattern; tympanum pale brown, encircled by a dark line; flanks lighter than dorsum, lighter ventrad and with dark spots; venter whitish, throat and chest with or without dark marking; distinct cross-bars on dorsal limbs; the rear of thigh with dark vertical bars (usually a continuation from dorsal surface and separated by narrow lighter areas) or mottling (dark marking on lighter background); ventral legs are dusted with brown pigment; webbing color brown. In preservative, dorsal background light brown; flanks becoming gray; iris changed to gray.

Variation. (1) number of tubercles on dorsum and flanks: few to dense; (2) size of tubercles on dorsum: small and round to larger and elongated; (3) dorsolateral fold absent, but row of few small tubercles form incomplete dorsolateral series, dorsal to the posterior of trunk (not in continuation of tympanic fold); (4) dorsal coloration: dark blotches on green background vary from few and isolated, to dense, and forming irregular green background network between the dark blotches; (5) flank color yellowish-green to green (as dorsum), lighter ventrad, with distinct spots; (6) upper and lower lips: whitish to greenish, with dark markings, small distinct bars to wide and connected, lip

Table 4. Morphometric values from all specimens of *Sumaterana* gen. n. examined in this study. Information given for each character as follows: average±st.deviation (first line), min–max (second line).

Character	*S. crassiovis* comb. n.		*S. montana* sp. n.		*S. dabulescens* sp. n.	
	(males, n = 96)	(females, n = 32)	(males, n = 10)	(females, n = 7)	(males, n = 27)	(females, n = 3)
SVL	37.58±4.01 30.03–48.87	67.43±10.42 40.98–83.99	29.98±1.14 27.94–31.56	55.07±2.58 51.61–59.60	37.65±1.45 34.69–40.86	57.30±7.58 48.03–66.60
HL	14.73±1.76 11.92–19.66	26.84±4.04 16.44–32.44	12.01±0.40 11.53–12.83	21.61±0.99 20.42–25.35	14.86±0.53 13.81–15.73	24.13±2.71 20.79–27.43
HW	13.52±1.66 10.96–18.61	24.43±3.72 14.14–29.68	10.88±0.53 9.74–11.79	19.61±1.09 18.04–21.65	14.00±0.59 12.99–15.20	23.03±2.78 19.41–26.18
SL	5.85±0.71 4.52–7.82	10.80±1.66 6.76–13.61	4.99±0.38 4.47–5.53	8.76±0.59 7.83–9.59	5.82±0.22 5.22–6.26	9.55±0.98 8.35–10.74
SN	2.26±0.26 1.78–2.99	3.92±0.64 2.50–5.82	2.15±0.35 1.73–2.77	3.95±0.60 3.11–4.80	2.21±0.14 1.94–2.47	3.39±0.40 2.88–3.85
EN	3.45±0.35 2.62–4.44	6.30±0.95 4.17–8.16	2.70±0.24 2.29–3.14	4.86±0.31 4.58–5.55	3.38±0.13 3.10–3.62	5.33±0.46 4.71–5.80
IND	3.78±0.44 3.03–5.17	6.52±0.94 3.79–7.90	3.50±0.33 3.06–4.01	6.10±0.75 5.04–7.58	3.79±0.19 3.44–4.26	5.95±0.50 5.25–6.40
IOD	3.49±0.34 2.90–4.53	6.13±0.88 4.05–7.99	3.23±0.19 2.96–3.51	5.21±0.40 4.72–5.94	3.41±0.16 3.02–3.76	4.93±0.70 4.03–5.74
UEW	4.07±0.62 2.72–6.05	6.84±1.10 4.18–8.48	2.96±0.18 2.72–3.22	5.21±0.40 4.65–6.00	4.02±0.34 3.41–4.67	5.63±0.56 4.90–6.26
ED	5.62±0.61 4.59–7.70	9.10±1.42 5.68–11.40	4.41±0.35 3.80–4.97	7.23±0.59 6.64–8.29	5.40±0.37 4.76–6.39	7.96±1.06 6.63–9.22
TYv	3.23±0.37 2.39–3.97	3.86±0.59 2.46–4.82	3.08±0.31 2.43–3.40	3.69±0.14 3.50–3.92	3.21±0.23 2.88–3.86	2.99±0.58 2.26–3.67
TYh	3.22±0.36 2.39–4.29	3.84±0.63 2.46–4.82	3.02±0.30 2.44–3.50	3.43±0.14 3.19–3.57	3.12±0.28 2.27–3.70	2.78±0.17 2.58–3.00
ET	1.14±0.29 0.74–2.90	2.74±0.64 1.44–4.01	0.92±0.12 0.70–1.17	2.14±0.17 1.87–2.31	1.20±0.11 1.01–1.50	2.07±0.19 1.90–2.33
LAL	8.26±0.75 6.89–10.06	14.43±2.03 9.00–17.13	7.05±0.31 6.49–7.58	11.63±0.74 10.08–12.45	8.11±0.31 7.74–9.11	12.23±1.23 10.71–13.73
HAL	13.14±1.34 10.77–16.82	23.27±3.34 14.90–30.32	10.85±0.46 10.26–11.72	18.70±0.98 17.41–20.79	12.48±0.42 11.62–13.33	18.25±1.58 16.11–19.87
FE	22.33±2.10 19.29–28.55	40.35±5.89 24.25–50.36	19.75±0.96 18.16–21.14	35.94±1.49 33.97–38.66	22.42±0.81 21.18–24.29	32.44±4.06 27.55–37.50
TL	24.52±2.61 20.74–31.85	44.61±6.31 27.83–55.96	22.17±0.90 20.96–24.20	40.69±1.13 38.29–42.08	23.74±0.72 22.30–25.30	36.01±3.32 31.46–39.28
FL	20.68±2.34 16.26–27.71	38.11±5.57 23.64–49.14	18.82±0.51 18.19–19.53	34.85±1.53 32.30–37.54	19.63±1.31 14.41–22.04	30.27±3.27 25.94–33.85
IMTL	1.75±0.27 1.28–2.62	3.20±0.57 1.72–4.29	1.50±0.13 1.30–1.70	2.70±0.30 2.30–3.27	1.83±0.16 1.51–2.10	2.74±0.26 2.38–2.96
F1L	3.88±0.51 3.02–5.30	7.77±1.34 4.62–10.90	3.46±0.18 3.19–3.84	6.78±0.55 6.07–7.73	3.78±0.18 3.28–4.05	5.62±1.50 3.52–6.96
F2L	4.85±0.59 3.92–6.74	8.89±1.39 5.85–11.79	3.66±0.19 3.30–3.96	6.99±0.53 6.26–8.00	4.55±0.22 4.17–5.19	7.03±0.80 6.01–7.97
F3DW	2.00±0.35 1.29–3.01	3.62±0.62 2.26–5.06	1.16±0.20 0.93–1.54	1.82±0.25 1.40–2.13	2.03±0.16 1.64–2.27	3.00±0.48 2.33–3.46
T4DW	1.36±0.30 0.92–2.26	2.71±0.46 1.72–3.47	1.08±0.21 0.78–1.40	1.82±0.17 1.63–2.20	1.58±0.13 1.30–1.77	2.43±0.32 1.99–2.76

markings absent or very thin in few individuals; (7) ventral dark markings: from none (ventral side whitish) to dark on throat and reaching venter, pale to dark; (8) rear of thigh with dark bars, complete or broken, or occasionally dark mottling on whitish/grayish background (Fig. 4a–d); (9) iris: golden to pale yellow, from faint and thin to dense and dark netting; (10) number of cross bars: 3–4 on lower arm (from elbow to wrist), 4–7 on thigh; (11) Toe IV: from one phalanx free of webbing to webbing reaching intercalary tubercle of Toe IV (Fig. 4e–h). See Fig. 8 for images of *Sumaterana crassiovis* comb. n. from different localities and for morphometric variation Tables 4–5.

Sexual dimorphism. Males significantly smaller than females. Tympanum diameter 45.27–71.68% ED in males, 33.33–48.51% ED in females. Male with distinct undi-

Table 5. Morphometric ratios from all specimens of *Sumaterana* gen. n. examined in this study. Information given for each character as follows: average±st.deviation (first line), min–max (second line).

Character	*S. crassiovis* comb. n.		*S. montana* sp. n.		*S. dabulescens* sp. n.	
	(males, n = 96)	(females, n = 32)	(males, n = 10)	(females, n = 7)	(males, n = 27)	(females, n = 3)
HW/ HL	91.80%±2.75% 86.44%–100.30%	90.97%±2.85% 84.36%–97.32%	90.61%±3.99% 82.85%–95.08%	90.72%±2.30% 87.54%–94.49%	94.21%±2.01% 88.32%–96.87%	95.37%±1.61% 93.36%–97.31%
SL/ ED	104.32%±8.80% 77.76%–125.45%	119.03%±7.66% 106.07%–138.71%	113.90%±13.48% 94.66%–145.53%	121.99%±14.12% 103.02%–144.43%	108.08%±7.18% 94.05%–120.59%	120.50%±3.99% 116.49%–125.94%
EN/ SN	153.27%±12.86% 119.60%–187.64%	162.54%±10.76% 141.08%–187.96%	127.22%±14.95% 107.60%–157.23%	125.25%±16.53% 100.00%–150.80%	153.19%±9.46% 140.27%–177.84%	157.58%±5.31% 150.65%–163.54%
IND/ IOD	108.15%±6.51% 95.83%–143.79%	105.48%±6.82% 91.11%–121.35%	108.01%±5.99% 99.71%–121.88%	116.74%±8.06% 106.78%–128.66%	111.38%±5.47% 102.65%–121.94%	121.74%±7.76% 111.50%–130.27%
IOD/ UEW	86.87%±9.24% 68.26%–120.31%	91.20%±9.72% 75.96%–124.80%	109.33%±3.46% 102.17%–114.14%	98.60%±6.15% 89.33%–105.48%	84.68%±7.10% 72.38%–100.00%	87.24%±3.88% 82.24%–91.69%
TYv/ ED	57.76%±5.57% 46.53%–71.68%	42.59%±3.72% 36.75%–56.83%	74.01%±10.69% 52.31%–89.47%	50.57%±6.19% 43.91%–60.47%	59.63%±4.62% 51.82%–72.94%	37.90%7±.28% 28.18%–45.70%
TYh/ ED	57.45%±5.37% 45.27%–71.68%	42.33%±3.80% 33.33%–56.83%	73.07%±11.60% 52.31%–92.89%	46.46%±4.08% 41.54%–54.67%	58.61%±4.30% 51.82%–69.36%	35.29%±2.68% 32.54%–38.91%
F1L/ F2L	80.08%±4.24% 70.56%–90.80%	86.72%±3.25% 78.97%–93.54%	94.55%±4.18% 87.67%–101.82%	97.05%±2.62% 93.46%–100.89%	83.41%±4.24% 78.03%–94.16%	78.45%±14.09% 58.57%–89.47%
F3DW/ T4DW	148.51%±15.60% 113.73%–197.03%	133.13%±9.69% 112.08%–160.09%	108.13%±8.45% 91.04%–120.00%	93.19%±11.74% 73.68%–108.12%	128.79%±8.42% 105.13%–144.53%	122.94%±4.16% 117.09%–126.38%
FE/ TL	91.16%±2.33% 85.82%–95.02%	90.39%±1.87% 85.39%–94.32%	89.10%±2.63% 85.17%–94.12%	88.33%±2.47% 85.09%–93.45%	94.43%±1.96% 89.40%–97.55%	89.85%±4.00% 86.51%–95.47%
HL/ SVL	39.17%±1.20% 36.22%–42.03%	39.88%±1.24% 37.52%–43.53%	40.09%±1.51% 37.83%–42.88%	38.84%±1.03% 37.16%–40.28%	39.49%±1.13% 37.66%–42.67%	42.22%±0.86% 41.19%–43.29%
HW/ SVL	35.96%±1.46% 33.06%–39.40%	36.27%±1.36% 33.57%–39.68%	36.31%±1.91% 33.66%–39.33%	35.22%±0.59% 34.16%–35.97%	37.20%±1.11% 34.95%–39.01%	40.26%±0.72% 39.31%–41.05%
SL/ SVL	15.56%±0.61% 13.99%–17.05%	16.01%±0.65% 14.70%–17.53%	16.65%±1.23% 14.95%–18.73%	15.74%±0.88% 14.42%–17.04%	15.49%±0.59% 14.46%–16.55%	16.73%±0.52% 16.13%–17.38%
SN/ SVL	6.02%±0.41% 4.81%–7.50%	5.77%±0.24% 5.31%–6.13%	7.18%±1.11% 5.66%–8.86%	7.09%±0.98% 6.01%–8.66%	5.89%±0.38% 5.04%–6.62%	5.93%±0.11% 5.78%–6.02%
EN/ SVL	9.18%±0.47% 8.27%–10.75%	9.37%±0.63% 8.41%–11.02%	9.00%±0.73% 7.44%–10.17%	8.72%±0.25% 8.30%–9.07%	9.00%±0.40% 8.32%–9.64%	9.36%±0.47% 8.71%–9.81%
IND/ SVL	10.06%±0.61% 8.67%–12.62%	9.69%±0.68% 8.05%–10.81%	11.66%±1.01% 10.62%–13.52%	10.91%±0.73% 9.75%–11.96%	10.04%±0.43% 9.23%–11.02%	10.46%±0.60% 9.61%–10.93%
IOD/ SVL	9.31%±0.46% 8.04%–10.75%	9.21%±0.64% 7.26%–10.33%	10.78%±0.51% 10.10%–11.91%	9.36%±0.42% 8.78%–9.96%	9.03%±0.49% 8.17%–10.13%	8.60%±0.16% 8.39%–8.78%
UEW/ SVL	10.81%±0.98% 7.73%–12.90%	10.15%±0.68% 7.73%–11.24%	9.87%±0.59% 8.90%–10.85%	9.50%±0.32% 8.99%–9.90%	10.72%±0.81% 9.18%–12.17%	9.87%±0.34% 9.40%–10.20%
ED/ SVL	14.99%±1.06% 12.82%–19.09%	13.50%±0.84% 11.92%–15.40%	14.72%±1.06% 12.16%–16.10%	13.00%±1.02% 11.80%–14.73%	14.37%±0.85% 12.64%–15.84%	13.88%±0.09% 13.80%–14.00%
TYv/ SVL	8.67%±0.83% 6.80%–10.79%	5.72%±0.45% 4.83%–6.63%	10.80%±1.12% 8.42%–12.96%	6.81%±0.39% 6.42%–7.54%	8.55%±0.52% 7.78%–9.67%	5.26%±0.98% 3.95%–6.31%
TYh/ SVL	8.62%±0.80% 6.42%–10.47%	5.68%±0.42% 4.84%–6.64%	10.73%±1.24% 8.42%–12.36%	6.28%±0.36% 5.68%–6.88%	8.41%±0.55% 7.65%–10.21%	4.90%±0.36% 4.50%–5.37%
ET/ SVL	3.03%±0.79% 2.23%–9.66%	3.98%±0.52% 3.12%–5.08%	3.05%±0.36% 2.38%–3.79%	3.83%±0.19% 3.62%–4.14%	3.18%±0.24% 2.78%–3.79%	3.65%±0.35% 3.32%–4.14%
LAL/ SVL	22.05%±1.22% 19.58%–25.46%	21.41%±1.12% 19.03%–24.18%	23.53%±0.70% 22.48%–24.48%	20.92%±1.52% 19.44%–24.12%	21.61%±0.83% 20.04%–23.05%	21.44%±0.69% 20.62%–22.30%
HAL/ SVL	35.01%±1.51% 31.77%–39.23%	34.47%±1.49% 31.54%–36.98%	36.20%±1.35% 34.17%–38.93%	33.61%±1.47% 30.93%–35.85%	33.26%±1.18% 31.08%–36.00%	32.06%±1.60% 29.83%–33.54%
FE/ SVL	59.54%±2.76% 53.83%–67.33%	59.84%±2.37% 54.62%–63.19%	65.86%±1.38% 63.23%–68.32%	64.63%±2.85% 60.35%–67.80%	59.65%±2.52% 54.95%–64.69%	56.67%±0.49% 56.31%–57.36%
TL/ SVL	65.32%±2.72% 58.78%–75.37%	66.22%±2.71% 60.17%–70.52%	73.97%±2.34% 70.88%–78.39%	73.29%±4.83% 65.28%–79.67%	63.17%±2.51% 58.08%–68.81%	63.20%±2.99% 58.98%–65.50%
FL/ SVL	55.06%±2.44% 49.18%–63.85%	56.46%±2.27% 50.91%–60.23%	62.82%±1.71% 59.52%–65.32%	62.69%±3.42% 57.38%–67.51%	52.25%±3.14% 39.59%–56.93%	53.01%±1.54% 50.83%–54.18%
IMTL/ T4DW	131.80%±22.06% 92.07%–212.77%	117.46%±14.34% 98.80%–150.00%	144.27%±33.28% 97.86%–212.82%	139.17%±19.24% 111.36%–171.78%	115.89%±10.10% 98.75%–138.69%	113.49%±6.59% 104.35%–119.60%

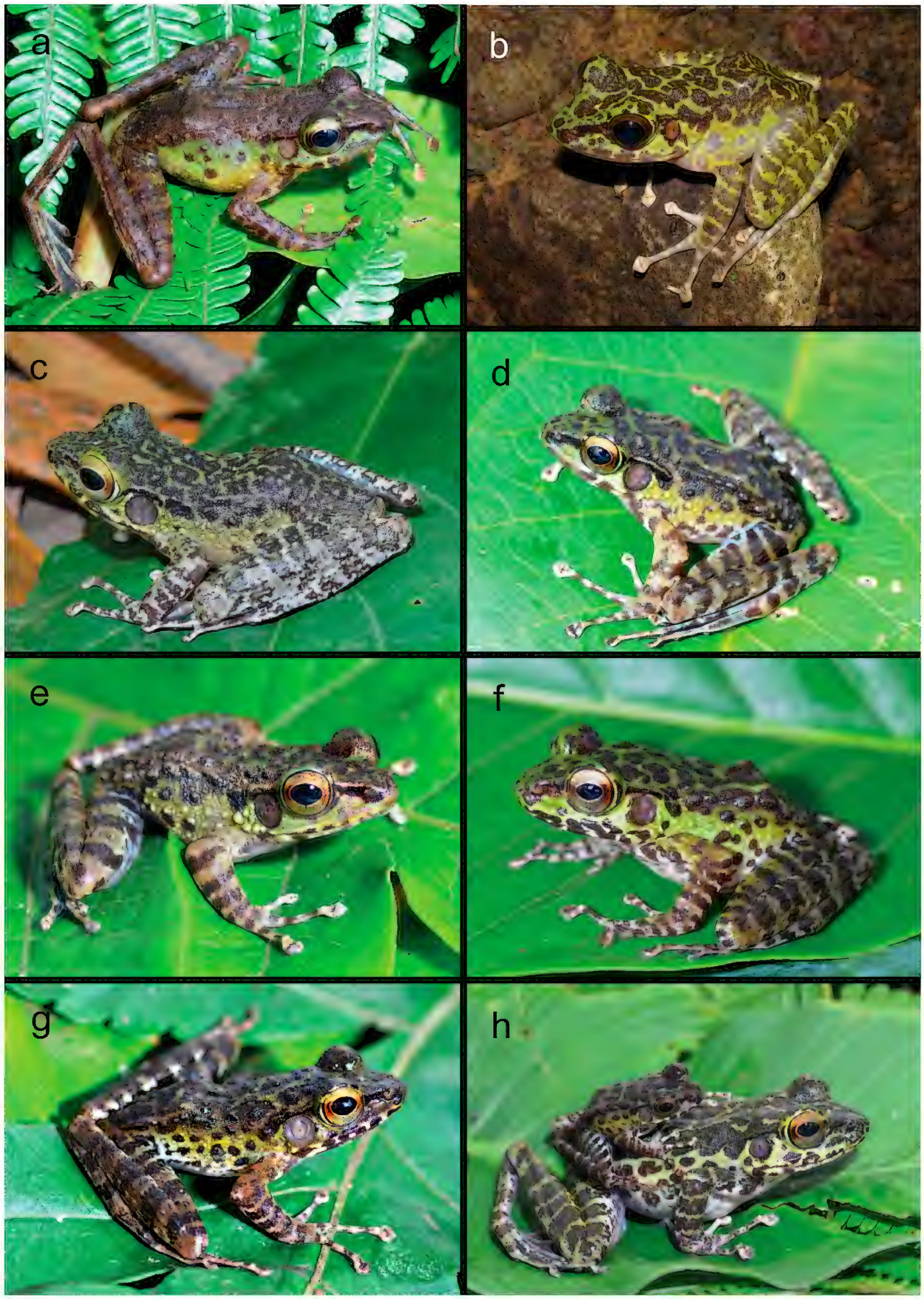

Figure 8. Morphological variation within *Sumaterana crassiovis* comb. n. (**a**) MZB.AMPH.29196, female, Provinsi Aceh, (**b**) Provinsi Sumatera Utara, (**c**) MZB.AMPH.29200, male, Provinsi Sumatera Barat, (**d**) ZMH.A14197, male, Provinsi Sumatera Barat, (**e**) MZB.AMPH.29320, male, Provinsi Sumatera Barat, (**f**) MZB.AMPH.29277, young male, Provinsi Bengkulu, (**g**) ZMH. A14151, male, Provinsi Sumatera Selatan, (**h**) ZMH.A14185 and MZB.AMPH.29296, male and female, Provinsi Lampung. Photos by U. Arifin, except for (b) by A. Irawan.

vided nuptial pads, covering base of the first finger to subarticular tubercle in dorsal and medial surface, paired subgular vocal sacs, humeral glands absent.

Common name. We propose Kerinci Cascade Frogs as the common English name (to replace the old spelling in "*Korinchi Frog*", Iskandar and Mumpuni 2004) and Katak Jeram Kerinci as the Indonesian name.

Distribution and ecological remarks. This species is widespread on the island of Sumatra, ranging from the northern part of Provinsi Aceh to Kabupaten Pasawaran, the southern part of Provinsi Lampung (Fig. 9). Elevational range 425–1545 m a.s.l.. This species is abundant along rocky streams (usually 1–5 m wide) in primary or good secondary forest. The inhabited streams are typically rocky with boulders (usually diameter > 1 m) and with rock formations along the stream, water current velocity 0.2–1.1 m/s (Fig. 10). Males of this species commonly can be observed perching on rocks or vegetation at the stream banks. Females were rarely observed near the streams. It seems that they approach the streams only during breeding activities. Tadpoles were often found in groups, on rocks in the stream, overflown with water in cascading sections.

Tadpoles. Tadpoles were identified (100%) using 12S rRNA+16S rRNA+tRNA^{val} barcoding with adult samples from the type locality. We examined total of 21 tadpoles. Stage 25: MZB.AMPH.29362 (n = 1), ZMH.A12649 (n = 3), MZB.AMPH.29363 (n = 1), MZB.AMPH.29364 (n = 1), Stage 26: MZB.AMPH.29362 (n = 2), MZB.AMPH.29356 (n = 1), ZMH.A12649 (n = 2), MZB.AMPH.29365 (n = 1), Stage 31: MZB.AMPH.29362 (n = 1), Stage 32: MZB.AMPH.29362 (n = 1), Stage 35: MZB.AMPH.29362 (n = 1), ZMH.A12650 (n = 1), Stage 36: MZB.AMPH.29355 (n = 1), ZMH.A12649 (n = 1), Stage 39: MZB.AMPH.29360 (n = 1), Stage 42: MZB.AMPH.29361 (n = 1). One selected tadpole from the lot had 100% match (12S rRNA+16S rRNA+tRNA^{val}) to an adult *Sumaterana crassiovis* comb. n. from the type locality. We refer to ZMH.A12650 (stage 35, Fig. 11a–c) for tadpole description.

Head and trunk approximately oval in dorsal view and dorsoventrally depressed and streamlined, in lateral view; maximum body width 64.40% body length; snout expanded and broadly rounded with emargination laterally setting off snout from body; eyes positioned dorsolaterally, oriented laterally; ED = 2.31 mm; IND/IOD = 48.22%; SN/EN = 44.82%; nostril open without raised rim; positioned anterodorsally and anterolaterally directed; two glands clusters present, infraorbital glands (five on each side) and postorbital glands (one on each side); oral disc ventral, a groove separating upper lip from snout, ODW/BW = 66.33%; oral disc marginal papillae short, arranged in single row; marginal papillae of upper lip present only on sides, on lower lip in uninterrupted row; two short submarginal papillae in lateral area of upper lip; LTRF: 9(6–9)/9(1); upper jaw sheath broad and heavily keratinized, smooth, undivided, thick but with distinct thinner medial section; lower jaw sheath undivided, V-shaped, smooth, and thick; both jaw sheaths finely serrated along their edges; very large abdominal sucker adjoining oral disc posteriorly, SUL/BL = 76.61%, SUW/BW = 89.03%; spiracle sinistral, tube long and posterior half free from body wall, opening directed posteriorly or posterodorsally; anal tube median, free from tail fin, directed posteriorly; strongly muscular tail: TAL/BL = 165.71%, TMH/BH = 71.87%, TMH/MTH = 63.00%; upper fin convex; maximum upper fin height is 30.57% maximum tail height at 49.19% of tail length; tail tip pointed.

In life (Fig. 11a–c), dorsum light brown, orangeish anteriorly and posteriorly to eyes; trunk darker than head; tail muscle light brown with fine-orange stippling; lower flanks region whitish; lateral tail vein very obvious, including dorsal branching along myosepta; upper and lower fins mostly transparent without iridophores; iris black, with dense gold to orange iridescent stippling; abdomen whitish laterally and densely stippled with fine-orange iridophores medially; abdominal sucker mostly transparent with white iridocytes in the center. In preservation, upper side gray with dark stippling; dense-dark stippling laterally; iris black; lens gray; ventral side uniformly transparent with some grey pigments in the anterior region of snout and lateral parts.

Sumaterana montana sp. n.

http://zoobank.org/72D3A049-2C2F-43FC-B38A-483C295BEC08

Figs 2 Clade B, 5c, 6c

Holotype. MZB.AMPH.29377 (female), Gunung Baru, Desa (=village) Seblat Ulu, Taman Nasional (=National Park) Kerinci-Seblat, Kabupaten Lebong, Provinsi Bengkulu, Sumatra, Indonesia (02.88413°S, 102.13073°E), 2033 m a.s.l., 4 May 2014, 20:44, coll. U. Arifin.

Paratypes (10). ZMH.A14194 (female, Fig. 5c and Fig. 6c), approx. 300 m from the holotype locality (02.88525°S, 102.12993°E), 2000 m a.s.l., 3 May 2014, 22:04, coll. U. Arifin and G. Cahyadi. MZB.AMPH.23516 (male) and MZB.AMPH.23517 (female), 02.55397°N, 098.59806°E, 1774 m a.s.l.; MZB.AMPH.23518 (female), UTA.A64829 (female), MZB.AMPH.23519 (male), MZB.AMPH.23520 (male), UTA.A64830 (male), UTA.A64831 (male), UTA.A64832 (male), 2.54691°N, 98.61414°E, 1780 m a.s.l.; vicinity of Tele, Kecamatan Samosir, Kabupaten Toba-Samosir, Provinsi Sumatera Utara, Indonesia, 20 January 2014, coll. E. N. Smith, M. I. Lubis, K. A. O'Connell, and E. Wostl.

Referred specimens (16). See Appendix 1.

Diagnosis. (1) medium sized frog, SVL males (n = 10) 27.94–31.56 mm and females (n = 7) 50.11–63.37 mm; (2) dorsum skin finely granulated, color generally brown with scattered light spots; (3) tympanum distinct and translucent, slightly deep, supratympanic fold present, posttympanic fold absent; (4) dorsolateral fold present, thin, continuation of supratympanic fold to the level of pelvic joint, uninterrupted

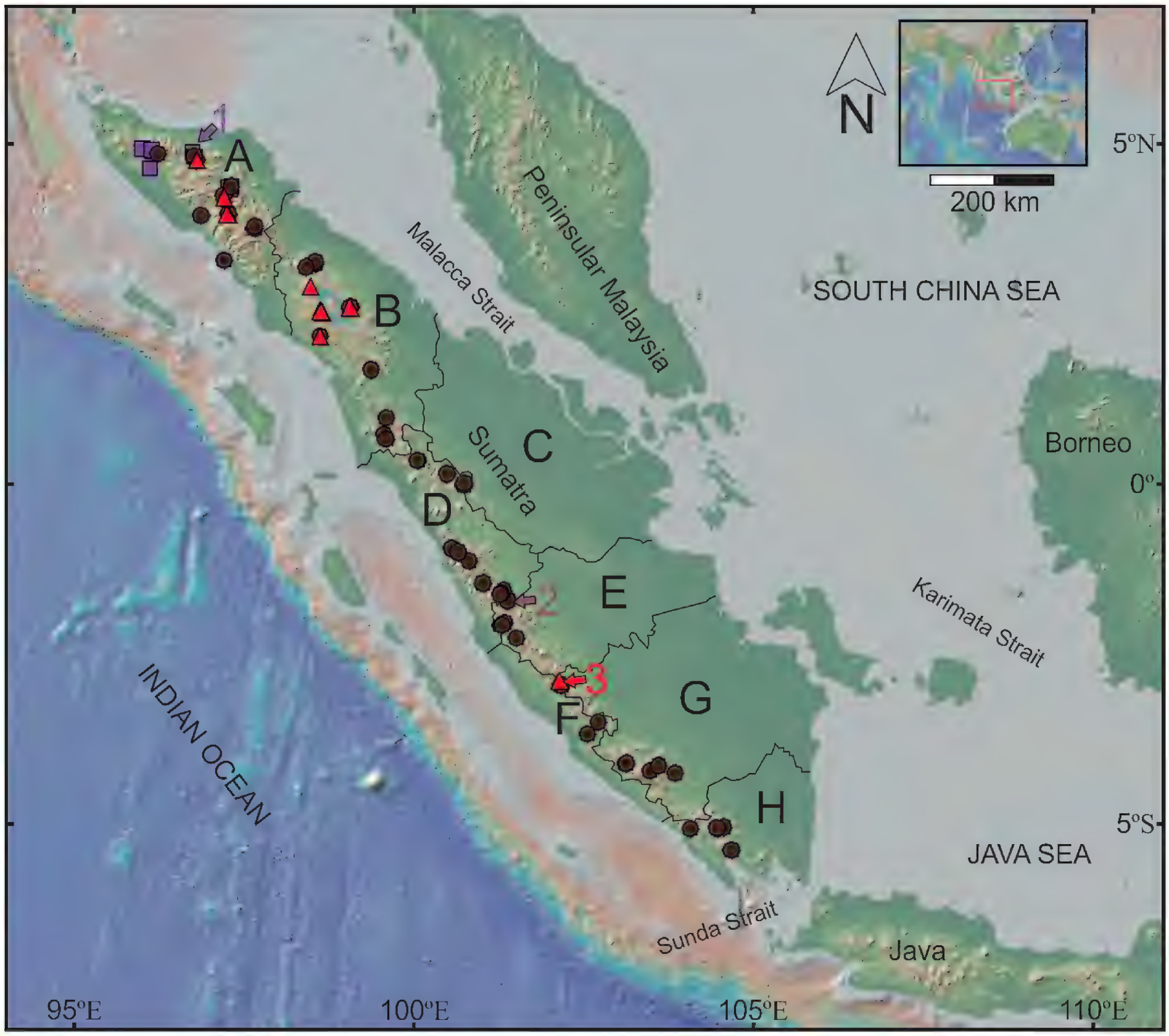

Figure 9. Geographical distribution of *Sumaterana dabulescens* sp. n. (purple squares; type locality purple arrow [**1**]: Jamat, Taman Buru Linge Isaq), *S. crassiovis* comb. n. (brown circles; type locality brown arrow [**2**]: Kerinci), and *S. montana* sp. n. (red triangles; type locality red [**3**]: Gunung Baru, Taman Nasional Kerinci-Seblat). The map was prepared using GeoMapApp (Ryan et al. 2009).

or broken; (5) venter smooth, white or yellowish; (6) tibia length 69.63–79.67% SVL; (7) Finger I 87.67–10.18% Finger II; (8) width of disc of Finger III 73.68–120.00% width of disc of Toe IV; (9) rear of thigh mottled; (10) approx. a quarter of the upper part of iris golden brown and the remaining iris with dense bright red stippling on black background; (11) webbing formula: I(0^{+}—$1^{1/2}$)II(0^{+}—2)III(0^{+}—3^{+})IV(3^{-}—0^{+})V; (12) outer metatarsal tubercle absent, inner metatarsal tubercle present; (13) males with paired vocal sacs, undivided nuptial pad, humeral gland absent.

Comparisons. *Sumaterana montana* sp. n. differs from *S. crassiovis* comb. n. (character in parentheses) in these characters: dorsum color brown with scattered light blotches (green background with dark markings on tubercles, lighter area forming irregular network pattern); iris golden brown in the upper quadrant, below with dense bright red stippling on back background (golden yellow with reddish color in the anterior and posterior sector and dark netting pattern); rear of thigh mottled, light spots on dark background (usually with vertical dark bars on lighter background, as continuation of dorsal thigh); dorsal texture shagreened, generally without tubercles (finely granulated with scattered tubercles); length of Finger I ≈ Finger II (Finger I < Finger II); disc width of Finger III ≈ disc width of Toe IV (disc width of Finger III > disc width of Toe IV); dorsolateral fold present, thin (absent); webbing formula: I(0^{+}—$1^{1/2}$)II(0^{-}—2)III(0^{-}—3^{+})IV(3^{-}—0^{+})V (I($1^{+/-}$—$1^{+/-}$)II($1^{+/-}$—$1^{+/-}$)III($1^{+/-}$—$2^{+/-}$)IV($2^{+/-}$—$1^{+/-}$)V).

Description of holotype. Adult female, gravid; body relatively slender; head width 91.93% head length; snout rounded, slightly pointed in dorsal view, and slightly protruding in lateral view; vomerine teeth present, in oblique groups, between choanae; loreal area deeply concave; canthus rostralis sharp, constricted behind nostrils; rictal ridge

present; eye-nostril distance 133.41% of snout-nostril distance; interorbital distance 99.00% width of upper eyelid; tympanum distinct, translucent, slightly set deep, diameter < 50% ED (TYv/ED = 49.31%, TYh/ED = 44.91%); supratympanic fold present, posttympanic fold absent; pineal spot visible; dorsolateral fold thin, starting in line with supratympanic fold anteriorly to the level of pelvic joint; dorsum and flank skin shagreened; venter skin smooth. Arm slender, lower arm length 19.44% SVL; hand length 32.81% SVL; fingers long, without webbing, tip extended into discs, diamond-like shaped, with circummarginal groove; length of Finger I 96.63% Finger II, Finger III longest; flaps present on the outer phalanges of all fingers; subarticular tubercles distinctive; disc width of Finger III 94.42% disc width of Toe IV. Hindlimbs long, articulation of the heels reach far beyond the tip of snout when limb aligned with body, relative length of femur, foot, and tibia to SVL: 61.01%, 69.63%, and 59.24%, respectively; toe lengths: I < II < III < V < IV, Toe V only slightly longer than Toe III; toe tip extended into diamond-shaped discs; cirmummarginal groove present; webbing formula: I(0^+—$1^{1/2}$)II(0^+—2)III(0^+—3^+)IV(3^-—0^+)V; subarticular tubercle distinct; inner metatarsal tubercle distinct, oval, 152.09% T4DW; outer metatarsal tubercle absent; tarsal fold absent.

Holotype coloration. In life, dorsum and upper head brown with scattered light spots; dark dorsolateral line from eye to groin; flanks brown lighting up ventrad, with yellowish color in the posterior region, and many round dark spots; venter yellowish, dark markings on throat up to half of abdomen; golden brown color in at the upper quarter sector of iris, the remaining parts of iris with dense red stippling on black background; a series of dark spots encircled base of upper eye lid; dark brown line from eye to nostril (along canthus rostralis) towards snout tip, not connected to counterpart at tip of snout; dark brown area between eye and tympanum; tympanum pale brown with darker spot in the center; upper lip background brown, lighter posteriorly, with dark brown spots; lower lip brown with few light spots; arm with four dark cross-bars, from elbow to wrist; dorsal face of thigh and tibia brown, each with 6 dark bars; yellow spots on groin; rear of thigh mottled, whitish and yellow spots on brown background; ventral skin of thigh dusted brown on cream background, denser on both lateral side of posterior region; webbing color brown. Color in preservative similar to life coloration; dorsum brown and markings remain the same; yellowish color on flanks and venter changed into white; iris color became gray.

Holotype measurements (mm). SVL 59.60, HL 23.35, HW 21.65, SL 9.14, SN 4.16, EN 5.55, IND 7.58, IOD 5.94, ED 7.95, UEW 6.00, TYv 3.92, TYh 3.57, ET 2.31, LAL 12.32, HAL 20.79, FE 38.66, TL 41.50, FL 37.54, IMTL 3.27, F1L 7.59, F2L 7.73, F3DW 2.03, T4DW 2.15.

Variation. (1) dorsum color background: light pale brown to dark brown; (2) lighter spots on dorsum, none to dense; variable size; (3) dorsolateral fold: continuous or interrupted, variable thickness; (4) yellowish posterior of flank; pale to brighter; (5) tubercles on flanks: none to many; (6) round dark spots on flanks, few to many; size: small to big; (7) dark marking on throat, chest, and ventrum: none to present and reaching the belly; (8) cross bars on limbs, 3–4 (arm, from elbow to wrist), 5–6 (thigh); variable thickness; (9) mottled pattern on rear of thigh: small, yellow and creamy spots to blotches, on brown background. (Metrics: Tables 4–5).

Sexual dimorphism. Males smaller than females. Tympanum diameter 52.31–92.89% ED in males and 41.54–60.47% ED in females. Adult males with single, undivided nuptial pad covering base of the first finger to subarticular tubercle on dorsal and medial surface. Paired subgular vocal sacs visible, humeral glands absent.

Etymology. The specific epithet is the Latin adjective *montana* in allusion to the distribution of this species at high elevations of the Bukit Barisan mountain range of Sumatra.

Common name. We propose Mountain Cascade Frogs as common English name and Katak Jeram Gunung in Bahasa Indonesia.

Distribution and natural history. Only known from high elevations of northern (Provinsi Aceh and Provinsi Sumatera Utara) and mid (Provinsi Bengkulu) Sumatra (Fig. 9). Known elevation was from 1190–2033 m a.s.l.. The holotype was perching on moss on a root of a dead tree, about 120 cm above a small creek (50 cm wide), ~50 m from Camp 4.5 of Gunung Baru, Desa Ulu Seblat, Taman Nasional Kerinci-Seblat, Kabupaten Lebong, Provinsi Bengkulu (~2000 m a.s.l.). The paratype ZMH.A14194 was observed sitting on the branch, about 300 m away, at the same creek where the holotype was collected, 200 cm above the ground. Accompanying fauna included species of *Rhacophorus* and *Philautus*. Paratypes from the vicinity of Tele, Kecamatan Samosir, Kabupaten Toba-Samosir, Provinsi Sumatera Utara were collected along the stream in the rainforest with patches of coffee plantation. The two specimens of *Sumaterana montana* sp. n. from the stream at Marpunge, Taman Nasional Gunung Leuser, Kabupaten Gayo Lues, Provinsi Aceh were found within low vegetation in the middle of the stream, *S. crassiovis* were abundant syntopically. Specimens from Gunung Sibuatan, Kabupaten Karo, Provinsi Sumatera Utara were found on the stream bank about 1–4 m away from water.

Tadpoles. Unknown.

Sumaterana dabulescens sp. n.

http://zoobank.org/A4E2A0F3-E0DA-43A1-BEEC-0340026C3BCB
Figs 2 Clade C, 5b, 6b

Holotype. MZB.AMPH.29396 (male, Fig. 5b), Desa Jamat, Taman Buru Linge Isaq, Kabupaten Aceh Ten-

Figure 10. (**a–b**) Typical cascading stream habitat of *Sumaterana crassiovis* comb. n. at Taman Nasional Gunung Leuser, Provinsi Aceh. *Sumaterana dabulescens* sp. n. inhabits similar stream habitats. (**c**) Specimen of *S. dabulescens* sp. n. on a rock near a small cascade in its natural habitat at Taman Buru Linge Isaq, Provinsi Aceh. Photos by U. Arifin.

gah, Provinsi Aceh, Sumatra, Indonesia (04.36482°N, 097.24783°E), 440 m a.s.l., 6 March 2014, 20:02, coll. U. Arifin and G. Cahyadi.

Paratypes (24). ZMH.A14159 (female, Fig. 6b) and MZB.AMPH.29398 (female) and five males MZB. AMPH.29400 (male), MZB.AMPH.29402 (male), ZMH. A14161–62 (males), ZMH.A12667 (male), same data as holotype, (20:00–21:31, except ZMH.A12667 at 13:00). UTA.A64917 (male), stream at Enang-Enang Resort, road of Takengon-Bierut, Provinsi Aceh, (04.88649°N, 096.72689°E, 604 m a.s.l.), 7 August 2015, 20:00–21:00, coll. E. N. Smith and F. Akhsani. UTA.A64919 (male), Kabupaten Bener Meriah, Provinsi Aceh, (04.82623°N, 096.74841°E), 924 m a.s.l., 6 August 2015, coll. I. Sidik and F. Akhasani. UTA.A64921 (male), 04.93841°N, 095.98375°E, 314 m a.s.l., UTA.A64922 (male) and UTA.A64923 (male), 04.93852°N, 095.98294°E, 323 m a.s.l., UTA.A64924 (male), 04.93869°N, 095.98250°E, 333 m a.s.l., Kruong Meuriam, Kecamatan Tangse, Kabupaten Pidie, Provinsi Aceh, 6 June 2016, I. Sidik and W. Trilaksono. MZB.AMPH.29381 (male), MZB. AMPH.29383 (male), MZB.AMPH.29385 (male), MZB. AMPH.29387 (male), MZB.AMPH.29389 (male), ZMH. A14154–58 (males), ZMH.A12668 (male), Kecamatan Mane, Kabupaten Pidie, Provinsi Aceh, (4.92091°N, 96.12275°E), 761 m a.s.l., 20 March 2014, coll. U. Arifin and G. Cahyadi.

Referred specimens (22). 13 adults, one juvenile, and 8 tadpoles (Appendix 1).

Diagnosis. (1) medium sized frog, SVL males (n = 27) 34.69–40.86 mm and females (n = 3) 48.03–66.60 mm; (2) dorsum finely granulated with scattered round, distinct tubercles; generally gray with dark gray spots on tubercles; (3) tympanum distinct and translucent (not transparent), supratympanic fold present, posttympanic fold absent; (4) dorsolateral fold absent; (5) venter smooth, granulated posteriorly, white; (6) tibia length 58.08–68.81% SVL; (7) Finger I 58.57–94.16 Finger II; (8) width of disc of Finger III 105.13–144.53% width of disc of Toe IV; (9) rear of thigh mottled; dark blotches on light background; (10) iris silver-gray with dark netting, slightly yellow to orange golden in the upper part; (11) all toes fully webbed to base of discs ($I(1^{+/-}—1^{+/-})II(1^{+/-}—1^{+/-})III(1^{+/-}—1^{+/-})IV(1^{+/-}—1^{+/-})V$); (12) outer metatarsal tubercle absent, inner metatarsal tubercle present; (13) males with paired vocal sacs, divided nuptial pad, humeral gland absent.

Comparison. *Sumaterana dabulescens* sp. n. differs from *S. crassiovis* comb. n. and *S. montana* sp. n. (character in parentheses: *S. crassiovis* comb. n.; *S. montana* sp. n.) by gray dorsum with dark markings on tubercles, lighter area forming irregular network pattern (green background with dark markings on tubercles, lighter area forming irregular network pattern; brown background with lighter sports, Fig. 5); iris color in life silver gray with dark reticulation, slightly yellow to golden in the upper part (golden yellow with reddish color in the anterior and posterior sector and dark netting pattern; golden brown in the upper quadrant of the iris, remaining iris with dense bright red stippling on black background; Fig. 3); rear of thigh mottled, dark blotches on light background (generally barred, dark bars on light background; mottled, light spots on dark background; Fig. 3); dorsal skin texture coarsely granulated with scattered round tubercle, vary in size and density (finely granulated with scattered tubercles, vary in size, shape, and density; shagreened, without tubercles); dorsolateral fold absent (absent; present, thin); length of Finger I < Finger II (Finger I < Finger II; Finger I ≈ Finger II); nuptial pad on male divided (undivided; undivided; Fig. 3); webbing full on all toes (I($1^{+/-}$—$1^{+/-}$)II($1^{+/-}$—$1^{+/-}$)III($1^{+/-}$—$2^{+/-}$)IV($2^{+/-}$—$1^{+/-}$)V; I(1—$1^{1/2}$)II(0—2)III(0—3)IV(3—0)V).

Description of holotype. Male, vocal sacs distinct and paired; nuptial pad distinct, divided, covering dorso-medial face of proximal Finger I to level of subarticular tubercle; humeral gland absent; body relatively slender; head width 90.11% head length; in dorsal view, snout obtusely pointed, in lateral view acutely projecting; canthus rostralis sharp, constricted behind nostrils; loreal area deeply concave; vomerine teeth present, in oblique groups, between choanae; tongue lanceolate; rictal ridge present; eye-nostril distance 177.84% snout-nostril distance; interorbital distance 89.27% width of upper eyelid; tympanum distinct, translucent, diameter > 50% ED (TYv/ED = 64.85; TYh/ED = 69.36%); supratympanic fold distinct, posttympanic fold absent; pineal spot visible; dorsolateral fold absent; dorsum and flanks finely granulated with scattered rounded tubercles on the dorsal region up to the upper part of the flanks; venter skin smooth, finely granulated in the posterior region; hindlimb long, articulation of the heels reach far beyond the tip of snout when limb aligned with body; thigh length 94.90% tibia; tibia 64.02% SVL; fingers slender, without webbing; Finger I 94.16% Finger II, Finger III longest; skin flaps present on the outer phalanges of all fingers; subarticular tubercles on fingers and toes distinct; disc width of Finger III 105.13% disc width of Toe IV; discs of toes and fingers diamond-shaped, both with circummarginal grooves; toe lengths: I < II < III < V < IV, Toe V slightly longer than Toe III; toes fully webbed; inner metatarsal tubercle distinct, oval, 118.59% T4DW; outer metatarsal tubercle absent; tarsal fold absent.

Holotype coloration. In life, dorsum and flanks generally gray; scattered tubercles on the dorsum and the upper part of flanks usually embedded in dark color; lighter area of the dorsum form an irregular network; golden color with dark spot between eye and nostril; upper lip grayish-white with dark spots (right: 4; left: 4); lower lip whitish with dark spots (right: 3; left: 2); iris silver-gray with dark netting, golden orange in the upper part; tympanum gray with light spot in the center; venter, chest, and throat fully whitish; forearm with four distinct dark cross-bars; hind limbs with thick dark cross-bars dorsally (thigh: 5; tibia: 5); rear of thigh with dark mottling on light gray background; legs light brownish ventrally; webbing brown. Dorsal coloration turned from gray with dark spots into uniformly dark brown in preserved specimens; flanks remained gray, lighter ventrad; iris color changed to uniform gray; no color change in the dark markings or pattern.

Holotype measurements (mm). SVL 36.13, HL 14.87, HW 13.40, SL 5.67, SN 1.94, EN 3.45, IND 3.88, IOD 3.66, ED 5.32, UEW 4.10, TYv 3.45, TYh 3.69, ETD 1.19, LAL 7.76, HAL 12.80, FE 21.95, TL 23.13, FL 19.19, IMTL 1.85, F1L 4.03, F2L 4.28, F3DW 1.64, T4DW 1.56.

Variation. (1) dorsum generally with round tubercles, lighter spots vary from few to dense; (2) number of dark-round tubercles on dorsum and flanks: few to many tubercles; (3) size of dark wound tubercles on dorsum and flanks: small to big tubercle; (4) life coloration of dorsum background: lighter grey or slightly grayish-green to dark gray; (5) iris upper sector: light yellow to orange; (6) dark netting of iris: loose to dense; (7) throat, chest, and venter with or without marking, ranging from none to marking reaching venter; (6) marking on upper and lower lip: variable in size; (9) number of cross bars on limbs: 2–4 (arm between wrist and elbow), 4–7 (thigh); (10) thickness of cross bars on limbs: variable; (11) composition of dark color on lighter background of mottling pattern on rear of thigh: dense to less dense dark pattern on lighter background. Metrics in Tables 4–5.

Sexual dimorphism. Males smaller than females. Tympanum diameter 38.54–72.94% ED in males and 28.18–45.70% ED in females. Adult males with divided nuptial pads and vocal sacs, covering dorso-medial face of proximal Finger I to level of subarticular tubercle, humeral gland absent.

Etymology. The species epithet *dabulescens* is an artificial construct of "*dabul*", "gray" in Gayo language, combined with the Latin ending "-*escense*", here in the sense of "tending to be", in allusion to the gray appearance of this species. The Gayo are a local tribe in the Aceh region of Sumatra and after which the Gayo highlands have been named.

Common name. We propose Gayo Cascade Frogs as the English common name and Katak Jeram Gayo as name in Bahasa Indonesia.

Distribution and natural history. Provinsi Aceh, particularly localities in the northern and middle part of Aceh:

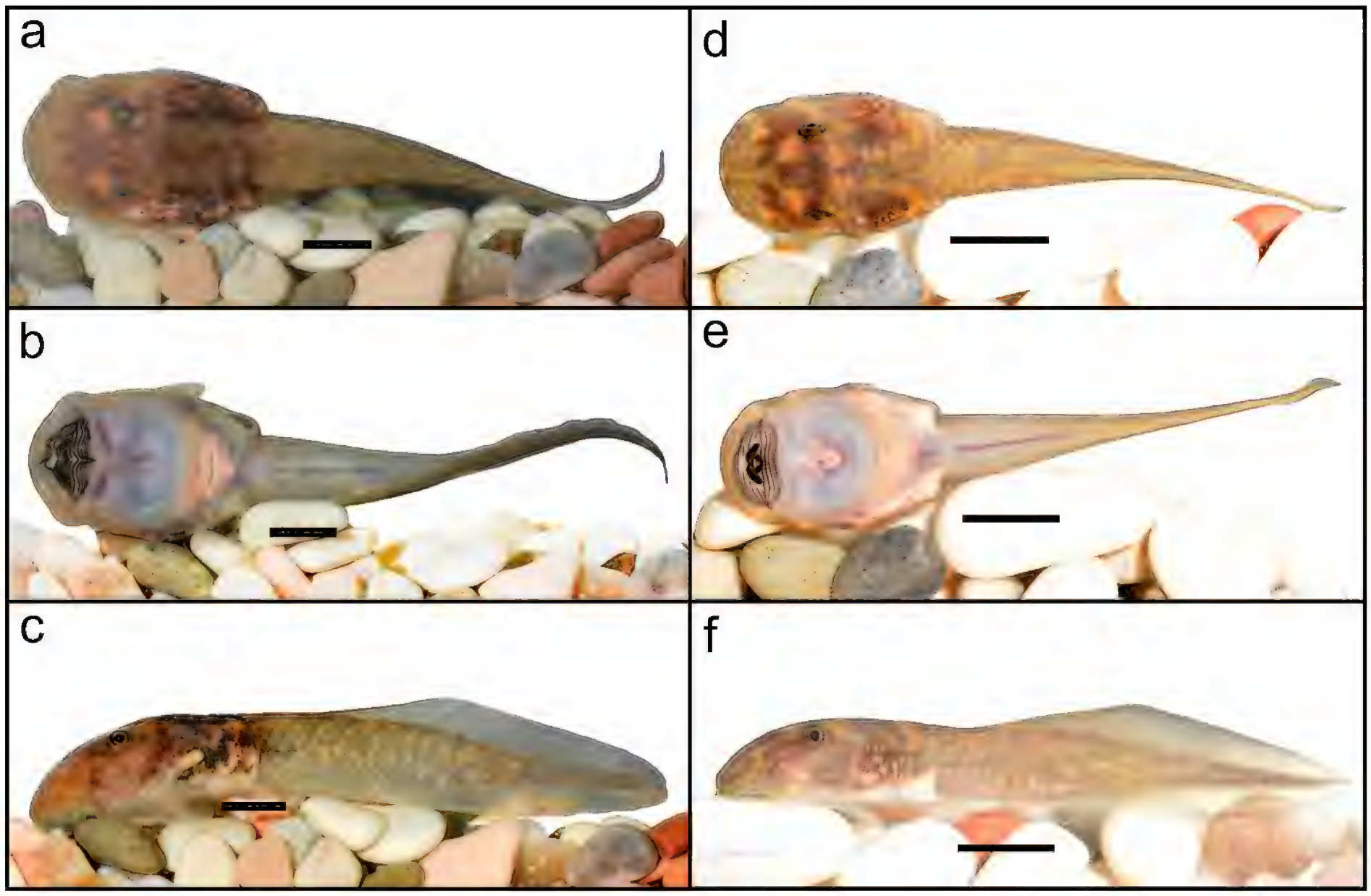

Figure 11. Tadpoles of *Sumaterana crassiovis* comb. n., ZMH.A12650, Provinsi Sumatera Barat (**a–c**) and *S. dabulescens* sp. n., MZB.AMPH.29411, Provinsi Aceh (**d–f**) showing dorsal, ventral, and lateral view. Scale 5 mm. Photos by U. Arifin.

Kecamatan Mane, Kabupaten Pidie; Krung Meuriam, Kecamatan Tangse, Kabupaten Pidie; Kabupaten Bener Meriah; Road Takengon-Bierut, Enang-Enang Resort, Kabupaten Aceh Tengah, and Taman Buru Linge–Isaq, Kecamatan Takengon, Kabupaten Aceh Tengah (Fig. 9). Known elevation for this species was 314–1000 m a.s.l.. The holotype was caught 100 cm above water level on a rock wall at the stream slope. The paratypes were perching on vegetation above the stream (15–200 cm above water) or on rocks in the stream or at the stream bank. The other specimens were collected from rocks or vegetation either in stream or approx. 30–100 cm away from the water (e.g., Fig. 10c). Tadpoles were collected between 23:00–24:00 from rocks (diameter ~1 m) in a fast flowing stream (4 m wide), local protected forest, Kecamatan Mane, Kabupaten Pidie.

Tadpoles. We examined eight tadpoles of *Sumaterana dabulescens* sp. n.. Stage 25: UA20140336 (n = 5), ZMH.A12655 (n = 1), Stage 28: MZB.AMPH.29411 (n = 1), Stage 37: MZB.AMPH.29413 (n = 1). Tadpole assignment to species was justified by 100% genetic match (12S rRNA+16S rRNA+ $tRNA^{val}$) of the selected tadpole to an adult from the same locality (Fig. 2). For the following description we refer to MZB.AMPH.29413 (Stage 37) because this specimen has the most advanced developmental stage in the series: in dorsal view, body slightly rectangular, snout broadly rounded, body rounded at both posterior corners; in lateral view, dorsoventrally depressed, streamlined; maximum body width 65.51% body length; eyes dorsolateral, oriented laterally; ED = 1.61 mm; IND/IOD = 48.01%; SN/ES = 45.23%; nostrils directed anterolaterally; nostril opens without raised rim; infraorbital gland cluster (left: 6 glands; right: 3) and postorbital gland cluster (two in each side) present; oral disc ventral, a groove separating upper lip from snout, oral disc width 68.00% body width; edge of oral sucker protruding snout contour in dorsal view; oral disc marginal papillae short, arranged in a single row; on upper lip marginal papillae present only on lateral parts, on lower lip in uninterrupted row; two short submarginal papillae in lateral area of upper lip; LTRF: 8(5–8)/8(1); upper jaw sheaths broad, heavily keratinized, smooth, undivided, thick but medial part conspicuously thinner than lateral parts; lower jaw sheaths undivided, smooth, V-shaped, thick; both jaw sheaths finely serrated along their edges; very large abdominal sucker in posterior continuation of oral disc, SUL/BL = 70.47%, SUW/BW = 82.94%; spiracle sinistral, tube long, posterior half free from body wall; spiracle directed posterodorsally; anal tube median, free from tail fin, directed posteriorly; strong muscular tail: TMH/BH = 76.19%, TMH/MTH = 66.74%; upper fin convex; maximum upper fin height is approx. 34.99% MTH at approx. 49.00% TAL; tail tip pointed.

In life, dorsal coloration of body and tail densely mottled with brown and golden blotches on a grayish background with dense fine dark stippling; lower flanks with a conspicuous wedge-shaped white area; tail muscle dark with dense-dark stippling overlain by yellowish-golden

to orange mottling; lateral tail vein visible in first third of tail, including dorsal branching along myosepta; upper and lower fin mostly transparent, stippled with melanophores, especially towards the fin margin; yellowish-golden stippling also present in the upper and lower fin; iris background color black, with dense golden to orange iridophore stippling; abdomen whitish laterally and densely stippled with golden iridophores medially; golden iridophores stippling also present in the anterior region of the snout and oral disc; abdominal sucker mostly transparent except for the central spot with golden iridocytes and scattered pigment along the rim. In preservative: color of dorsal region became gray with dense darker dots and dark brown mottling; darker region were obvious on the upper flanks and between eyes and naris; iris all black; lens grayish-white; ventrally uniformly transparent with dark pigments in the anterior region of snout, oral disc, and lateral.

Body proportions between Stage 25, Stage 28, and Stage 37 were variable, e.g., BW/BH in Stage 25 (165.01%) > in Stage 28 (160.72%) > in Stage 37 (144.97%); SUW/BW in Stage 25 (89.58%) > in Stage 28 (86.66%) > in Stage 37 (82.94%); TAL/BL in Stage 25 (153.74%) < Stage 37 (174.06%) < in Stage 28(183.00%); TMH/BH in Stage 25 (61.38%) < in Stage 37 (76.19%) < in Stage 28 (84.71%); TMH/MTH in Stage 25 (60.53%) < in Stage 37 (66.74%) < in Stage 28 (71.00%). Variation: Body shape in the Stage 25 and Stage 28 were oval; the posterior region gradually arched towards the end of the body (e.g. Stage 28; Fig. 11d–f). Color patterns were also variable among the specimens. For example, in life, MZB.AMPH.29411 (Stage 28, Fig. 11d–f) had less mottling on upper side of body and tail than MZB.AMPH.29413 (Stage 37), more extensive golden color in the iris, smaller orange blotches in the tail region, very few golden spots in both upper or lower fin region, golden iridopores and pigments were less in the ventral region. In preservative, MZB.AMPH.29411 is lighter than MZB.AMPH.29413.

Species keys of *Sumaterana* sp. n. in the context of Southeast Asian Ranidae

1 Highly stream-adapted, gastromyzophorous tadpoles abdominal sucker present 2
– Abdominal sucker absent ..... *Abavorana*, *Amnirana*, *Chalcorana*, *Clinotarsus*, *Hylarana*, *Odorrana*, *Pulchrana*, *Staurois*
2 Expanded, rounded finger and toe tips ..... *Amolops*
– Expanded finger and toe tips, pointed and diamond shaped 3
3 Posttympanic and dorsolateral folds well developed, thick dark ∏-shaped over tympanum ..... *Huia*
– Posttympanic and dorsolateral folds well developed, no thick dark ∏-shaped over tympanum, endemic to Borneo ..... *Meristogenys*
– Posttympanic fold absent, dorsolateral folds present or absent, no thick dark ∏-shaped over the tympanum, endemic to Sumatra ..... 4, *Sumaterana*
4 Poorly developed dorsolateral folds, F1 subequal to F2 in length, F3DW subequal to T4DW, dorsum shagreened, brown, sometimes slightly tuberculate ..... *S. montana*
– Dorsolateral folds absent, F1 shorter than F2, F3DW wider than T4DW, dorsum green or greyish with darker markings, finely granulated and tuberculate 5
5 Undivided nuptial pad in males, green dorsal background in life, rear of thighs with dark bars ..... *S. crassiovis*
– Divided nuptial pad in males, gray dorsal background in life, rear of thighs with dark mottling or blotches ..... *S. dabulescens*

Conclusive summary

The taxonomic status of the taxon previously known as *Chalcorana crassiovis* has been problematic for a long time. The case was confounded by the description of a morphologically similar species (*C. kampeni*), the loss of the *C. kampeni* type specimen, insufficient sampling, and a lack of evidence beyond morphology (*viz.*, molecular data). After the original description by Boulenger (1920), only Inger and Iskandar (2015) collected substantial numbers of specimens from that taxonomic group. The exclusively morphological evidence in their validated the existence and provided a re-description of *C. crassiovis*, while questioning the existence of *C. kampeni*. Some authors still continue treating *C. crassiovis* and *C. kampeni* as distinct species, by implication of other evidence. Our study is the first to conduct molecular analyses for these doubtful taxa in a phylogenetic context. Our phylogenetic hypotheses strongly support *C. crassiovis* as a distinct lineage, and a diverse, monophyletic group (Fig. 2) that is not closely related to other species previously assigned to the genus *Chalcorana*. Our comprehensive sampling along the Sumatran transect yielded specimens with astonishing genetic diversity and morphological differences among the clades comprising the *crassiovis*-group (Fig. 2). We recommend all taxa in Clades A–C to be moved to the proposed new genus *Sumaterana* gen. n.. The new genus currently comprises three known species: *S. crassiovis* comb. n., *S. montana* sp. n. and *S. dabulescens* sp. n.. We consider them to represent valid species (*viz.*, independently evolving lineages) as indicated by genetic, morphological, and ecological differences in comparison to other related species (see above). Furthermore, our molecular data reveal the presence of gastromyzophorus larvae in the species belonging to *Sumaterana* gen. n..

Samples from the type localities of *Sumaterana crassiovis* comb. n. and "*Chalcorana kampeni*" were nested in Clade A in the phylogenetic analysis (Fig. 2) with small amounts of genetic divergence (uncorrected *p*-distance 2.56%, Suppl. materials 3). Furthermore, Inger and Iskandar's (2005) morphological description of *C. crassiovis* and Boulenger's (1920) original description matched our Clade A samples well, except for small differences. For example, according to Inger and Iskandar (2005) the tubercles on the dorsum were large and rounded, but in our samples some tubercles were also elongated and variable in size. Inger and Iskandar (2005) noted Finger I equal or slightly longer than Finger II, but in our samples Finger I was consistently shorter than Finger II. This may partially be attributed to different methods of finger length comparison. Inger and Iskandar (2005) reported skin flaps on the outer phalanges of the second and third fingers. We observed flaps present on the outer phalanges of all fingers, although not all of them are movable. This character is difficult to express unambiguously in verbal form (i.e., some may consider them fringes rather than flaps) and graded character states can occur on different fingers. Thus, we do not believe our observations contradict Inger and Iskandar (2005). Based on low genetic divergence within Clade A, morphological homogeneity among samples corroborating the original description of the type (Boulenger 1920) and the re-description by Inger and Iskandar (2005), and the inclusion of topotypic specimens of both previously named taxa, we recommend "*C. kampeni*" be considered a junior synonym of *S. crassiovis* comb. n..

In this study we included four known species of *Huia* (*H. cavitympanum*-type species, Borneo; *H. sumatrana*, Sumatra; *H. masonii*, Java; and *H. melasma*, the mainland Asia). Nevertheless, we were unable to solve the phylogenetic problem of *Huia*, which has previously been considered paraphyletic (Stuart 2008, Pyron and Wiens 2011). Our study perpetuates this conundrum as the type species of *Huia* (*H. cavitympanum*) was shown to be the sister taxon to Bornean *Meristogenys* in our analyses, rather than monophyletic with the other *Huia* species in our dataset. One possibility would have been to subsume all members of the assemblage (*Sumaterana* gen. n., *Meristogenys*, *Huia*, and *Clinotarsus*) under one name (*Clinotarsus*, the oldest available name). We did not choose this option in order to ensure taxonomic stability and because valuable biological information associated with the current monophyletic groups would be dissolved in one genus, such as island endemism (*Sumaterana* gen. n./*Meristogenys*), differences in adult and tadpole morphology and tadpole peculiarities (species of today's *Clinotarsus* with non-gastromyzophorous tadpoles). Because of the low support in parts of his tree, Stuart (2008) refrained from taxonomic amendments concerning *Huia*, and so do we. Much more effort needs to be invested to solve the perplexing phylogenetic uncertainties concerning *Huia*.

Another interesting subject arises from the optimized phylogenies in our analyses (Fig. 2) with respect to the evolution of larval gastromyzophory in Southeast Asian ranids. Previously all Asian ranid taxa with gastromyzophorous tadpoles were grouped under the genus *Amolops* (Inger 1966). Yang (1991) split the group into *Amolops*, *Huia*, and *Meristogenys* based on adult and tadpole morphological characters. Molecular systematic studies, however, suggested that the assemblage of *Amolops*, *Huia*, and *Meristogenys* was para- or polyphyletic (Frost et al. 2006, Stuart 2008, Pyron and Wiens 2011). Our phylogenetic analyses indicate that gastromyzophorous tadpoles have likely evolved independently, once in the most recent common ancestor of the group *Huia*+*Sumaterana* gen. n.+*Meristogenys* and again in the ancestor of *Amolops*. Tadpoles from both clades are perplexingly similar morphologically (Noble 1929, Gan et al. 2015), yet molecular evidence implies separate origins. Interestingly, although *Clinotarsus* does not possess gastromyzophorous tadpoles, this genus is nested within *Huia*+*Sumaterana* gen. n.+*Meristogenys* (Stuart 2008, Pyron and Wiens 2011, this study). Therefore, it could be hypothesized that larval gastromyzophory might have been lost secondarily in *Clinotarsus*. Further studies are needed to test and understand the evolution of this larval type in these frogs.

A third case of ranids with gastromyzophorous tadpoles has been reported in *Rana sauteri* (Boulenger, 1909). Its tadpoles are clearly more morphologically (Kuramoto et al. 1984) and biogeographically (Taiwan) distant to *Amolops*, *Huia*, and *Meristogenys*. Gan et al. (2015) summarized that in *R. sauteri* the edge of the abdominal sucker was not as sharply defined as in *Amolops*, *Huia*, and *Meristogenys* (sucker is completely free and rim raised), particularly at the posterior. Moreover, the sucker seems to work differently in *R. sauteri*: the musculus diaphragmatopraecordialis is absent in *R. sauteri*, but well developed in *Amolops*, *Huia*, and *Meristogenys* (Gan et al. 2015, Kuramoto et al. 1984). Finally, other body features of *R. sauteri* (relatively narrow oral sucker and extensive dorsal tail fin) underline the morphological differences between this and to other Asian gastromyzophorous tadpoles, implying possible separate origins and different adaptive scenarios.

We are fully aware that phylogenetic and taxonomic problems persist in our studied taxa. These need to be addressed in the future. Broad thorough geographic sampling of adult and larval forms is a prerequisite to solve phylogenetic quandaries with any amphibian taxa, especially in the species rich tropical realm. Moreover, integrating independent sources of evidence (e.g. DNA, morphology, distribution) is an optimal strategy to accurately and convincingly validate the taxonomic position of doubtful amphibian taxa from hyperdiverse hotspots (Dayrat 2005, Padial et al. 2009, Padial et al. 2010). Distantly related frog species that converged onto similar morphotypes (i.e., ecomorphs) are common in tropical biodiversity hotspots (Bossuyt and Milinkovitch 2002) and can confound taxonomic decisions; examples are documented in Stuart (2008).

Our results are also further evidence that the taxonomic diversity of Sumatran frogs is still significantly underestimated (Iskandar and Colijn 2000, Stuart et al. 2006, Inger et al. 2009), despite the recent increase of am-

phibian species described from the island (e.g. Teynie et al. 2010, Matsui et al. 2012, Hamidy and Kurniati 2015, Smart et al. 2017, Wostl et al. 2017). This also holds true for other herpetofauna, such as reptiles (Orlov and Ryabov 2002, David and Das 2003, Das 2005, Harvey et al. 2015, Wostl et al. 2016). Large scale and strategic sampling efforts are of the utmost priority in order to reveal the true faunal diversity and distribution patterns on this incredibly biodiverse island.

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Appendix 1

Specimens examined

(* bold = measured, star (*) = sequenced)

Sumaterana crassiovis comb. n. (adults, n = 262)

Provinsi Aceh. – Kabupaten Pidie, Mountain above Geumpang, Transmigrasi community, old road to mining camp, 4.85824°N, 96.21348°E, 1090 m a.s.l., UTA.A64868; Kabupaten Bener Meriah, road between Bireun-Takengon, 4.82623°N, 96.74841°E, 924 m a.s.l., UTA.A64856-60; Kabupaten Bener Meriah, foot of Berni Terlong, near Desa Rambune, pantan Pediangah, Tihmang gagah, 4.76379°N, 96.78131°E, 1184 m a.s.l., UTA.A64853; Kabupaten Aceh Tengah, Taman Buru Linge-Isaq, 4.37958°N, 97.29158°E, 1000 m a.s.l., **MZB.AMPH.29196, MZB.AMPH.29198, ZMH.A14168–69**; Kabupaten Gayo Lues, Kampung Ise-Ise, 4.25511°N, 97.18366°E, 1129 m a.s.l., UTA.A64855; Kabupaten Gayo Lues, Kedah, Blangkajeren, Rain Forest lodge, 3.97806°N, 97.25314°E, 1376 m a.s.l., UTA.A64851, UTA.A64852; Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser, 3.79289°N, 97.64417°E, 1190 m a.s.l., **MZB.AMPH.29188, MZB.AMPH.29190, MZB.AMPH.29192, MZB.AMPH.29194, ZMH.A14216–17, ZMH.A14219**; Kabupaten Nagan Raya, Road from Nagan Raya to Terangun, 3.95839°N, 96.85218°E, 795 m a.s.l., UTA.A64864–66; Kabupaten Aceh Selatan, Gunung Putri Tidur near Tapak Tuan, 3.2921°N, 97.19642°E, 481 m a.s.l., UTA.A64867; Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser, 3.77103°N, 97.63801°E, 1065 m a.s.l., **MZB.AMPH.29186*, ZMH.A14218.**

Provinsi Sumatera Utara. – Kabupaten Dili Serdang, Sungai DAM Bumi Perkemahan Sibolangit, 3.27347°N, 98.53586°E, 881–965 m a.s.l., **MZB.AMPH.29326***, MZB.AMPH.29327–29, **MZB.AMPH.29330–37**; Kabupaten Dili Serdang, Sungai Batu Belah Bumi Perkemahan Sibolangit, 3.27522°N, 98.53613°E, 880–965 m a.s.l., MZB.AMPH.29338–39, **MZB.AMPH.29340–41**, MZB.AMPH.29342–44; Kabupaten Dili Serdang, Sungai Derek Bumi Perkemahan Sibolangit, 3.27688°N, 98.53472°E, 877–908 m a.s.l., MZB.AMPH.29345–47, Kabupaten Karo, sungai Taman Wisata Alam Deleng Lancuk, 3.19668°N, 98.39298°E, 1416–1427 m a.s.l., MZB.AMPH.29348–49, **MZB.AMPH.29350**, MZB.AMPH.29351, **MZB.AMPH.29352**, MZB.AMPH.29353–54; Kabupaten Karo, Kecamatan Berastagi, Air Terjun Sikulikap, 3.24047°N, 98.53878°E, 1156 m a.s.l., **MZB.AMPH.23492–93**, UTA.A64879–81; Kabupaten Toba Samosir, Gunung Pangulubao, 2.60514°N, 99.04629°E, 1397 m a.s.l., **MZB.AMPH.23496–97**, **MZB.AMPH.23506**, **UTA.A64833***, UTA.A64882–86; Kabupaten Hambung Hasundutan, Gunung Pinapan, 2.18325°N, 98.60513°E, 1309 m a.s.l., MZB.AMPH.23498; Kabupaten Tapanuli Selatan, slope of Gunung T. Anjing, 1.68449°N, 99.34737°E, 1253 m a.s.l., MZB.AMPH.23505; Kabupaten Mandiling Natal, Huta Baringin Julu, Taman Nasional Batang Gadis, 0.66636°N, 99.57191°E, 1271 m a.s.l., UTA.A64894–902, **MZB.AMPH.23507–11**, **UTA.A64835***, **MZB.AMPH.23513–14**; Kabupaten Mandailing Natal, slope of Dolok Malea above Kampung Mompang, 0.97500°N, 99.57959°E, 991 m a.s.l., **MZB.AMPH.23499–501, MZB.AMPH.23503–04**, UTA.A64887–93; Kabupaten Mandailing Natal, road between Panyabungan and Natal, 0.72544°N, 99.54497°E, 804 m a.s.l., MZB.AMPH.23490–91.

Provinsi Sumatera Barat. – Kabupaten Pasaman, Kecamatan Panti, Stream 3 Cagar Alam Rimbo Panti, 0.35220°N, 100.04933°E, 425 m a.s.l., **MZB.AMPH.29200*, MZB.AMPH.29202, MZB.AMPH.29204, ZMH.A14170–73**; Kabupaten Pasaman, Kecamatan Panti, Stream 1 Batu Ampar, Cagar Alam Rimbo Panti, 0.35056°N, 100.04490°E, 450–500 m a.s.l., **MZB.AMPH.29206, MZB.AMPH.29208, MZB.AMPH.29210, ZMH.A14191–92**; Kabupaten Pasaman, Kecamatan Panti, Stream 1 Batu Ampar, Cagar Alam Rimbo Panti, 0.34789°N, 100.03748°E, 1000 m a.s.l., MVZ271526*; Kabupaten Payakumbuh, Kecamatan Pangkalan Koto Baru, Road from Payakumbuh to Pangkalan, 0.01905°N, 100.72205°E, 621 m a.s.l., UTA.A64847; Kabupaten Payakumbuh, small creek next to main road connecting Payakumbuh-Riau, 0.01916°S, 100.72226°E, 606–624 m a.s.l., **MZB.AMPH.29320*, MZB.AMPH.29322, MZB.AMPH.29324, ZMH.A14223–25**; Kabupaten Solok, Kecamatan Gunung Talang, Stream 1 Lubuak Sulasiah, 0.95782°S, 100.57112°E, 1040–1084 m a.s.l., MZB.AMPH.29212, MZB.AMPH.29214, MZB.AMPH.29216, MZB.AMPH.29218, MZB.AMPH.29220, MZB.AMPH.29222, MZB.AMPH.29224, ZMH.A14206–13; Kabupaten Solok, Kecamatan Gunung Talang, Stream 2 Lubuak Sulasiah, 0.94529°S, 100.54630°E, 1104 m a.s.l., MZB.AMPH.29226; Kabupaten Solok, Kecamatan Gunung Talang, Desa Kayu Jao, 0.99717°S, 100.63952°E, 1270 m a.s.l., ZMH.A14195; Kabupaten Solok, Kecamatan Gunung Talang, Stream 1 Desa Kayu Jao, 0.99557°S, 100.64334°E, 1315–1350 m a.s.l., MZB.AMPH.29228, MZB.AMPH.29230, ZMH.A14198; Kabupaten Solok, Kecamatan Gunung Talang, Stream 2 Kayu Jao, 0.99980°S, 100.63550°E, 1195 m a.s.l., MZB.AMPH.29232, MZB.AMPH.29234, ZMH.A14221–22; Kabupaten Solok, Road from Kayu Aro-Padang near Surian, 1.13573°S, 100.80255°E, 1417 m a.s.l., MZB.AMPH.22341, UTA.A62438; Kabupaten Solok Selatan, Muara Labuh, Taman Nasional Kerinci Seblat, 1.45534°S, 101.00020°E, 640–643 m a.s.l., **MZB.AMPH.29253, MZB.AMPH.29255, ZMH.A14136–37** Kabupaten Solok Selatan, Padang Aro, Taman Nasional Kerinci Seblat, 1.559317°S, 101.31072°E, 605 m a.s.l., **ZMH.A14197***; Kabupaten Solok Selatan, Batang Blangir, Padang Aro, Taman Nasional Kerinci Seblat, 1.61750°S, 101.24780°E, 975 m a.s.l., **MZB.AMPH.29237, MZB.AMPH.29241, MZB.AMPH.29243, MZB.AMPH.29245, MZB.AMPH.29247, MZB.AMPH.29239, ZMH.A14179–84**; Kabupaten Solok Selatan, stream at the foot hill of Lake Bontak, Taman Nasional Kerinci Seblat, 1.60325°S, 101.26391°E, 850 m a.s.l., MZB.AMPH.29249, MZB.AMPH.29251, ZMH.A14226–28.

Provinsi Jambi. – Kabupaten Kerinci, trail to Danau Tujuh, 1.71076°S, 101.36986°E, 1506 m a.s.l., MZB.AMPH.22221, MZB.AMPH.22222, MZB.AMPH.22223, MZB.AMPH.22334, UTA.A64904, UTA.A64905, UTA.A64906; Kabupaten Kerinci, road between Sungai Penuh and Tapan, west of crest, 2.04139°S, 101.31462°E 1250 m a.s.l., MZB.AMPH.22345; Kabupaten Kerinci, Gunung Kunyit, Taman Nasional Kerinci-Seblat, 2.26013°S, 101.49512°E, 1355 m a.s.l., **MZB.AMPH.22336**, **MZB.AMPH.22338**, **MZB.AMPH.22339***, **MZB.AMPH.22340**,

UTA.A64907–13; Kabupaten Kerinci, Bukit Tapan, Taman Nasional Kerinci Seblat, 2.06988°S, 101.26235°E, 726 m a.s.l., MZB.AMPH.29257; 2.06543°S, 101.26771°E, 787 m a.s.l., ZMH. A14193; Kabupaten Kerinci, Sungai Kunyit, Bukit Tapan, Taman Nasional Kerinci Seblat, 2.06925°S, 101.28656°E, 909–916 m a.s.l., MZB.AMPH.29259, MZB.AMPH.29261, MZB. AMPH.29263, MZB.AMPH.29265, MZB.AMPH.29267, MZB. AMPH.29269, ZMH.A14201–05.

Provinsi Bengkulu. – Kabupaten Lebong, Stream at Camp 2 Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.95330°S, 102.13955°E, 758-774 m a.s.l., **ZMH.A14166–67, MZB. AMPH.29271**; Kabupaten Lebong, Stream at Camp 3 Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.95100°S, 102.16345°E, 716–723 m a.s.l., **MZB.AMPH.29273**, **MZB.AMPH.29275***, **MZB.AMPH.29277**; Kabupaten Lebong, Stream at Camp 1 Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.95330°S, 102.13955°E, 723 m a.s.l., **MZB.AMPH.29276**, **ZMH.A14165**.

Provinsi Sumatera Selatan. – Kabupaten Pagar Alam Selatan, road from Manna to Pagar Alam, 4.11296°S, 103.10007°E, 772 m a.s.l., UTA.A64870, UTA.A64873–75, UTA.A64877; Kabupaten Muara Enim, Gunung Patah near Desa Segamit, 4.21742°S, 103.46823°E, 1545 m a.s.l., UTA.A64849; Kabupaten Muara Enim, Sungai Lematan Desa Batu Surau, 4.13725°S, 103.58640°E, 1048–1069 m a.s.l., **MZB.AMPH.29312, MZB.AMPH.29314, MZB.AMPH.29316, MZB.AMPH.29318, ZMH.A14149*, ZMH.A14150–53**; Kabupaten Ogan Komering Ulu Selatan, Kecamatan Kisam Tinggi, Gunung Nanti, Desa Gunung Megang, 4.24586°S, 103.83415°E, 1048–1062 m a.s.l., **MZB. AMPH.29302, MZB.AMPH.29304, MZB.AMPH.29306, MZB.AMPH.29308, ZMH.A14140–43, MZB.AMPH.29310**; 4.24543°S, 103.8352°E, 874 m a.s.l., **ZMH.A14139***.

Provinsi Lampung. – Kabupaten Lampung Barat, Curug Berdua, Gunung Abung, Desa Purajaya, 5.03730°S, 104.54828°E, 956–979 m a.s.l., **MZB.AMPH.29282, MZB. AMPH.29284, MZB.AMPH.29286, MZB.AMPH.29288*, MZB.AMPH.29290**, **ZMH.A14144–48**; Kabupaten Lampung Barat, Sumber Jaya, 5.04456°S, 104.44930°E, 1022 m a.s.l., MZB.AMPH.29292, MZB.AMPH.29294, ZMH.A14214–15; Kabupaten Lampung Barat, Road Liwa to Krui, 5.06458°S, 104.05465°E, 673 m a.s.l., MZB.AMPH.22344, MZB. AMPH.22343, UTA.A62440; Kabupaten Lampung Barat, Sungai Pauh, Gedong Surian, 5.06651°S, 104.46261°E, 935–961 m a.s.l., ZMH.A14200, MZB.AMPH.29279, ZMH.A14199; Kabupaten Tanggamus, Air Terjun Talang Ogan, 5.37933°S, 104.66043°E, 754–717 m a.s.l., **MZB.AMPH.29296, MZB. AMPH.29298, MZB.AMPH.29300, ZMH.A14185*–86, ZMH.A14188, ZMH.A14186**.

Sumaterana crassiovis comb. n. (tadpoles, n = 21)

Provinsi Sumatera Barat. – Kabupaten Lima Puluh Koto, Desa Tanjuang Bungo, 0.15188°N, 100.47468°E, 388 m a.s.l., **MZB. AMPH.29363**; Kabupaten Payakumbuh, Stream next to the road between Payakumbuh-Riau 0.01917°S, 100.72226°E, 600–627 m a.s.l., **MZB.AMPH.29355***, **MZB.AMPH.29356, ZMH.A12649** (n = 6); Kabupaten Solok Selatan, Muara Labuh, Taman Nasional Kerinci-Seblat, 1.45534°S, 101.00020°E, 640–643 m a.s.l., **MZB.AMPH.29359, ZMH.A12650***; Kabupaten Solok Selatan, Kecamatan Sangir, Desa Padang Aro, Taman Nasional Kerinci-Seblat, 1.61750°S, 101.24780°E, 975 m a.s.l., **MZB.AMPH.29361, ZMH.A12651, ZMH.A12652** (n = 5).

Provinsi Sumatera Selatan. – Kabupaten Muara Enim, Desa Batu Surau, 4.13725°S, 103.58640°E, 1048-1069 m a.s.l., **MZB. AMPH.29364**, **MZB.AMPH.29365***.

Sumaterana montana sp. n. (adults, n = 28)

Provinsi Aceh. – Kabupaten Bener Meriah, foot of Berni Terlong, near Desa Rambune, pantan Pediangah, Tihmang gagah, 4.77054°N, 96.79341°E, 1377 m a.s.l., UTA.A64930; Kabupaten Gayo Lues, Stream Along Road S. (up) from Ise-Ise, 4.22357°N, 97.18655°E, 1827 m a.s.l., UTA.A64931, UTA.A64932, UTA. A64933, UTA.A64934; Kabupaten Gayo Lues, Stream in Lemon Grass Plantation, 3.97234°N, 97.23405°E, 1638 m a.s.l., UTA. A64935; Kabupaten Gayo Lues, Kedah, Blangkajeren, Rain forest lodge, 3.9771°N, 97.25256°E, 1355 m a.s.l., UTA.A64929; Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser, 3.79289°N, 9.764.417°E, 1190 m a.s.l., MZB.AMPH.29375, **ZMH.A14164***.

Provinsi Sumatera Utara. – Kabupaten Karo, Gunung Sibuatan, Above Kampung Naga Linga, 2.91076°N, 98.46313°E, 1625 m a.s.l., **MZB.AMPH.23522–24, UTA.A64834***, UTA. A64929; Kabupaten Toba Samosir, Gunung Pangulubao, 2.60441°N, 99.04599°E, 1392 m a.s.l., UTA.A64927; UTA. A64926; Kabupaten Samosir, vicinity of Tele, 2.55397°N, 98.59806°E, 1774 m a.s.l., **MZB.AMPH.23516*** (paratype), **MZB.AMPH.23517** (paratype), **UTA.A64829** (paratype); 2.54691°N, 98.61414°E, 1780 m a.s.l., **MZB.AMPH.23518–20** (paratype)**, UTA.A64830–32** (paratype); Kabupaten Simalungung, Simpang Tele, 2.52733°N, 98.63364°E, 1800 m a.s.l., Kabupaten Hambung Hasundutan, 2.18325°N, 98.60513°E, 1309 m a.s.l., UTA.A64928.

Provinsi Bengkulu. – Kabupaten Lebong, Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.88525°S, 102.12993°E, 2000 m a.s.l., **ZMH.A14194** (paratype); 2.88413°S, 102.13073°E, 2033 m a.s.l., **MZB.AMPH.29377*** (holotype).

Sumaterana dabulescens sp. n. (adults, n = 38)

Provinsi Aceh. – Kabupaten Pidie, Krueng Meriam, Tangse, 4.938417°N, 95.98375°E, 314 m a.s.l., **UTA.A64921** (paratype); 4.93852°N, 95.98294°E, 323 m a.s.l., **UTA.A64922** (paratype)**, UTA.A64923** (paratype); Kabupaten Pidie, Kecamatan Tangse, Stream along Tangse-Geumpang road, 4.93869°N, 95.9825°E, 333 m a.s.l., **UTA.A64924** (paratype); Kabupaten Pidie, Desa Mane, 4.92091°N, 96.12275°E, 761 m a.s.l., **MZB. AMPH.29381** (paratype)**, MZB.AMPH.29383** (paratype), **MZB.AMPH.29385** (paratype)**, MZB.AMPH.29387**(paratype)**, MZB.AMPH.29389** (paratype), **ZMH.A14154-58** (paratype)**, UA.2014.0397** (paratype); 4.91926°N, 96.12300°E, 747 m a.s.l., **MZB.AMPH.29392, MZB.AMPH.29384, ZMH.A14187, ZMH.A14190**; 4.89949°N, 96.13168°E, 700 m a.s.l., **ZMH.A14188**; Kabupaten Aceh Tengah, Road Takengon-Bierut, Enang-Enang Resort, 4.88649°N, 96.72689°E, 604 m a.s.l., **UTA.A64917** (paratype), UTA.A64918; Kabupaten Bener Meriah, 4.82623°N, 96.74841°E, 924 m a.s.l., **UTA.A64919** (paratype); Kabupaten Pidie, Road Tutut

to Geumpang, 4.65267°N, 96.09203°E, 593 m a.s.l., UTA. A64920; Kabupaten Aceh Tengah, Sungai Air Jambu, Taman Buru Linge Isaq, 4.36482°N, 97.24783°E, 440 m a.s.l., **MZB. AMPH.29396*** (holotype)**, MZB.AMPH.29398** (paratype)**, MZB.AMPH.29400** (paratype)**, MZB.AMPH.29402** (paratype)**, ZMH.A14159** (paratype)**, ZMH.A14161–62** (paratype)**, UA.2014.0214** (paratype); Kabupaten Aceh Tengah, red water stream, Taman Buru Linge Isaq, 4.37958°N, 97.29158°E, 1000 m a.s.l., **ZMH.A14163**; Kabupaten Aceh Tengah, Taman Buru Linge-Isaq, 4.338036°N, 97.28096°E, 600 m a.s.l., **MZB. AMPH.29405, MZB.AMPH.29407–09, ZMH.A14174**;.

Sumaterana dabulescens sp. n. (juvenile, n = 1)

Provinsi Aceh. – Kabupaten Pidie, Kecamatan Mane, Desa Mane, 4.92334°N, 96.12215°E, 792 m a.s.l., **MZB.AMPH.29378***.

Sumaterana dabulescens sp. n. (tadpoles, n = 8)

Provinsi Aceh. – Kabupaten Pidie, Kecamatan Mane, Stream 3 Mane, 4.91926°N, 96.12300°E, 747 m a.s.l., **MZB. AMPH.29410** (n = 5)**, MZB.AMPH.29411*, ZMH.A12655, MZB.AMPH.29413**.

Supplementary material 1

List of sequences and GenBank accession number

Authors: Umilaela Arifin, Utpal Smart, Stefan T. Hertwig, Eric N. Smith, Djoko T. Iskandar, Alexander Haas

Data type: molecular data

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Link: https://doi.org/10.3897/zse.94.22120.suppl1

Supplementary material 2

Illustration of morphological characters

Authors: Umilaela Arifin, Utpal Smart, Stefan T. Hertwig, Eric N. Smith, Djoko T. Iskandar, Alexander Haas

Data type: species data

Explanation note: Illustration of morphological characters measured in this study: A) for adults, B) for tadpoles. Explanation for each acronym available in Tables 2 and 3. Illustration by L. Waser.

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Link: https://doi.org/10.3897/zse.94.22120.suppl2

Supplementary material 3

Pairwise genetic distance

Authors: Umilaela Arifin, Utpal Smart, Stefan T. Hertwig, Eric N. Smith, Djoko T. Iskandar, Alexander Haas

Data type: molecular data

Explanation note: Pairwise genetic distance (uncorrected p) within crassiovis-group and all taxa used in this study based on 16S sequence, calculated using MEGA 7.1.025. Values are in percentage (%).

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